

Seasonal foraging behavior of Weddell seals in relation to oceanographic environmental conditions in the Ross Sea, Antarctica

5

Hyunjae Chung^{1, 2†}, Jikang Park^{3, 4}, Mijin Park^{1, 2}, Yejin Kim^{1, 5}, Unyoung Chun⁶, Sukyoung Yun⁴, Won Sang Lee⁴, [Hyun A Choi⁷](#), [Ji Sung Na⁴](#), Seung-Tae Yoon^{7, 8*}, Won Young Lee^{1, 9*†}

¹Division of Life Sciences, Korea Polar Research Institute, Incheon 21990, Republic of Korea

10 ²Department of Biological Sciences, Seoul National University, Seoul 08826, Republic of Korea

³Department of Biology, Kyung Hee University, Seoul 02447, Republic of Korea

⁴Division of Glacial Environment Research, Korea Polar Research Institute, Incheon, 21990, Republic of Korea

⁵School of Earth and Environmental Sciences, Seoul National University, Seoul 08826, Republic of Korea

⁶Division of EcoScience, Ewha Womans University, Seoul 03760, Republic of Korea

15 ⁷School of Earth System Sciences, College of Natural Sciences, Kyungpook National University, Daegu 41566, Republic of Korea

⁸Kyungpook Institute of Oceanography, Kyungpook National University, Daegu 41566, Republic of Korea

⁹Polar Science, University of Science and Technology, 217 Gajeong-ro, Daejeon, 34113, Republic of Korea

Correspondence to:

20 Seung-Tae Yoon, School of Earth System Sciences, College of Natural Sciences, Kyungpook National University, Daegu 41566, Korea

Email: styoona@knu.ac.kr

Won Young Lee, Division of Life Sciences, Korea Polar Research Institute, Incheon 21990, Korea.

Email: wonyounglee@kopri.re.kr

25 [†]Current Address:

Division of Glacial and Earth Sciences, Korea Polar Research Institute, Incheon, 21990, Republic of Korea

Abstract

Understanding the foraging behavior of marine animals in Antarctica is crucial for assessing their ecological significance and responses to environmental changes, such as. ~~Marine animals, in particular, In the context of Antarctica, marine animals face rapid and profound environmental changes in Antarctica, where related with global warming seasonal ocean circulation water mass changes in seawater, sea ice cover, and or or diurnal light hours variability are prominent photic conditions.~~ However, studying our understanding of their responses to these seasonal changes remains limited owing challenging due to the difficult logistics of formidable challenges inherent in conducting observations, particularly during the harsh austral winter months. In this study, we investigated the influence of changes in seawater properties and light conditions on the seasonal foraging behavior of Weddell seals (*Leptonychotes weddellii*) in the Ross Sea, Antarctica. We affixed 35 Weddell seals with CTD tags for three consecutive years from 2021 to 2023 to record their locations and dive profiles, including depth, head acceleration, temperature, and salinity. We found that seals foraged more frequently in modified shelf water and ice shelf water compared to than in Antarctic surface water. This preference could be connected to greater food availability. ~~Additionally, seals~~ Seals also dove to greater depths and displayed increased activity in capturing prey during daylight hours. This behavior may correspond to the diel vertical migration of pelagic prey in response to varying light conditions. ~~As a result~~ Consequently, marine fauna were confronted with distinct seasonal changes in the Antarctic environment and have adjusted their foraging behaviors to adapt respond to these changes them. ~~In the Antarctic environment, marine fauna are confronted with seasonal changes related to variations in water masses or diurnal light hours~~ Our findings suggest that Weddell seals have adjusted their foraging behaviors to adapt respond to spatial and temporal changes in oceanographic conditions. This highlights the importance of extrinsic factors in estimating their seasonal foraging behavior.

Keywords

Dive behavior, foraging habit, CTD, seal-tagging, bio-logging

In the Antarctic ecosystem, marine animals must adapt to environmental changes in the Antarctic ecosystem, such as seawater changes in sea water conditions and light availability fluctuations. Extrinsic factors play a vital role in their foraging success and food availability, particularly specifically under the challenging conditions they face rapid changes such as oceanic warming, complex bathymetry and changing sea-ice covers (Speakman et al., 2020; Harcourt et al., 2021; Arce et al., 2022). Therefore, understanding how marine animals adapt to spatial and temporal shifts in oceanographic conditions is of utmost importance paramount. Antarctic animals are currently experiencing rapid environmental change (Schofield et al., 2010; Doney et al., 2011). Glacier melting and the associated oceanic changes pose significant challenges for these animals (Huang et al., 2011; Ainley et al., 2015; Sahade et al., 2015; Hückstädt et al., 2020). As top and mesopredators, marine mammals animals serve as indicators of such for drastic changes. For example, calving on the Nansen Ice Shelf in the Ross Sea offers provides Adélie penguins (*Pygoscelis adeliae*) had explored a newly exposed sea after calving of ice shelf for additional foraging habitats with potentially high prey availability (Park et al., 2021), and Southern elephant seals (*Mirounga leonine*) and Weddell seals (*Leptonychotes weddellii*) had been reported to shift their seal movemnets and diving behaviors are influenced by foraging locations and depths with the species, sea ice extent, and oceanographic conditions all influence seal movements and diving behaviors (Bailleul et al., 2007; Labrousse et al., 2021).

The Ross Sea is the world's largest (2.09 million km²) Marine Protected Area (MPA) worldwide owing to its ecological significance (Brooks et al., 2021). It also stands as Antarctica's the largest continental shelf region in Antarctica. Because of its limited human accessibility, the Ross Sea has been preserved as a primary habitat for predatory animals, maintaining a pristine ecosystem because of its limited human accessibility (Smith et al., 2012). Notably, 40% of the world's Weddell seals (*Leptonychotes weddellii*), 38% of Adélie penguins, and 26% of emperor penguins (*Aptenodytes forsteri*) worldwide, along with a majority of South Polar skuas (*Stercorarius maccormicki*) in the Pacific sector, reside in the Ross Sea (La-Rue et al., 2021; Smith et al., 2012). In the coastal polynyas of the Ross Sea, dense shelf water, a parent water mass of the Antarctic Bottom Water (AABW), is formed by strong polynyal activity (Rusciano et al., 2013; Yoon et al., 2020). This water mass contributes approximately a quarter to the total AABW production in Antarctica (Orsi et al., 1999; Orsi and Wiederwohl, 2009; Jendersie et al., 2018; Silvano et al., 2023). Hydrographic observations have been actively conducted in the Ross Sea since the 1950s, revealing changes in its marine environment resulting from due to recent climate shifts (Jacobs et al., 2002; Castagno et al., 2019; Yoon et al., 2020; Silvano et al., 2020; Thomas et al., 2020; Yoon et al., 2020). According to these observations, hydrographic variations in the Ross Sea, including changes in the properties of shelf water, respond sensitively to air-sea interactions driven by katabatic winds and the advection of meltwater or sea ice from the Amundsen Sea (Rusciano et al., 2013; Castagno et al., 2019; Piñones et al., 2019; Yoon et al., 2020; Silvano et al., 2020; Yoon et al., 2020). It is anticipated that climate-induced variations in the marine environment of the Ross Sea are anticipated to could significantly impact the behavior of marine mammals. However, our understanding of their responses remains limited due to logistical and technological challenges.

Recent technological advancements in technology, employing miniaturized CTDs, have enabled researchers to monitor sea-water temperature and salinity (Kokubun et al., 2021; McMahon et al., 2021; Zheng et al., 2021). Deep-diving seals have mainly been used in oceanographic observation studies, with seal-tagging datasets being shared among researchers, particularly within the realm of polar ocean studies (Treasure et al., 2017). In addition to physical oceanographic data, behavioral data, such as diving patterns and acceleration serve as valuable indicators for estimating underwater foraging. Detailed feeding indices can be estimated from foraging diving depths and prey capture movements (Viviant et al., 2010; Volpov et al., 2015; Heerah et al., 2019; Nachtsheim et al., 2019; Aubone et al., 2021; Viviant et al., 2010; Heerah et al., 2019; Volpov et al., 2015; Photopoulou et al., 2020; Aubone et al., 2021).

Weddell seals are resident and primarily forage within the continental shelf of the Ross Sea (Goetz et al., 2023; Harcourt et al., 2021; Goetz et al., 2023). Within this region, their primary diet consists of fish (notothenioids), supplemented by minor dietary components such as cephalopods and invertebrates (Dearborn, 1965; Plötz et al., 1991; Burns et al., 1998; Dearborn, 1965; Goetz et al., 2017; Plötz et al., 1991). They are

100 ranked as the ~~second~~ deepest diving phocid species ~~with the exception of~~ except the southern (*Mirounga*
leonina) and northern after the southern elephant seals (*Mirounga leonina* and *Mirounga angustirostris*).
105 Hence, Weddell seals have been used to collect oceanographic and behavioral data at depths exceeding 600 m
(Heerah et al., 2013; Zheng et al., 2021). These seals endure energetically demanding periods during the austral
spring and autumn (October–February) seasons, marked by colony formation for pup birthing, rearing pups,
breeding, and molting, often leading to considerable weight loss (Wheatley et al., 2006; Harcourt et al., 2007;
Wheatley et al., 2008; Harcourt et al., 2007). Although both male and female Weddell seals sporadically forage
during the reproductive season, they are classified as capital breeders that rely on energy reserves accumulated
before breeding (Goetz et al., 2017; Harcourt et al., 2007; Wheatley et al., 2008; Goetz et al., 2017). Consequently,
110 the overwintering period (February–September) may be critical for seals to replenish their body mass and
condition.

In this study, we aimed to ~~present~~ examine the foraging behavior of Weddell seals ~~according to~~ in
association with the ~~temporal~~ seasonal changes during Antarctic summer to winter seasons (March to July) ~~in~~
hydrographic factors using acceleration-combined CTD data ~~obtained~~ from seal-tagging observations during the
Antarctic summer to winter (March to July) in the Ross Sea. By categorizing different water masses, we examined
115 ~~whether seals displayed~~ seasonal preferences of the seals for specific water masses ~~and if these preferences~~
varied seasonally. In addition, we estimated foraging behavior in response to daylight conditions.

2. Materials and Methods

2.1 Study area and CTD deployment

120 We conducted seal-tagging in January or early February of 2021, ~~and~~ 2022, and 2023 along the shores of Jang
Bogo Station (74°37'26" S, 164°13'44" E) and Gondwana Station (74°38'7" S, 164°13'18" E) situated in Terra
Nova Bay, Ross Sea, Antarctica (Fig. 1). We approached Weddell seals on the shore to deploy 35–57 CTD-Satellite
Relay Data Loggers (CTD-SRDs) or 7 CTD-SRDs with GPS (weight: 545 g, size: 105 × 70 × 40 mm, SMRU, UK). ~~Of~~
Among the 35–57 CTD-SRDs affixed to individuals (19, 16, and 22 in 2021, ~~and~~ 16 in 2022, and 2023
125 respectively), 55 ~~33~~ were attached to their head, and two were secured to their backs. Additionally, seven CTD-
SRDLs (five in 2021 and two in 2022) with GPS technology were attached to their backs. ~~Of~~ Among the 64 seals,
27 were identified to be females, and 35 were males based on their morphological features ~~feature~~. while
Two were not clearly distinguished in the field; hence, these ~~so that the two individuals were excluded in~~ from
the model analysis for comparing the sexes (for details, see Supplementary Table 1), and the sex of 2 seals could
130 not be determined because their ventral side could not be observed. These devices ~~are equipped with~~ have
temperature, conductivity, and pressure sensors, which collect ~~hydrographic~~ hydrographic data. According to the
specifications of the sensors of CTD-SRD, the accuracy of temperature, pressure, and conductivity are ±
0.005 °C, 2 dBar, and ±0.01 mS/cm⁻¹ (<https://www.smru.st-andrews.ac.uk/Instrumentation/CTD/>, last access:
20 May SMRU Instrumentation, 2024). However, low-resolution vertical profiles used in this study have a
135 relatively lower accuracy of ±0.04 °C for temperature (±0.04 °C) and salinity (±0.03 g/kg) ~~an accuracy of~~
±0.03 g/kg for salinity (Siegelman et al., 2019). ~~The sea water temperature was recorded with an accuracy of~~
0.005 °C, pressure (depth) with an accuracy of 2 dBar, and conductivity with an accuracy of 0.01 mS/cm. All data
obtained from CTD-SRDs were received via Argos satellites and no instruments were recovered. Detailed
information on the tagged individuals is provided in Supplementary Table 1.

140 Before deployment, we used an anesthetic (Zoletil®50, Virbac Laboratoires, Carros, France Zoletil 50;;
a combination of 125 mg tiletamine and 125 mg zolazepam in a 50 ml solution) administered through a blowpipe.
Following the injection, we waited for over 10 minutes until the seals were sufficiently sedated ~~we allowed for a~~
sedative effect, maintaining a distances from the seals for over 10 min. Once the seals exhibited no response to
the researcher's approach, we proceeded to affix a CTD device to the seal's head using Loctite glue (Loctite 401
145 was used in 2021; Loctite 422 in 2022 and 2023 ~~Loctite 401 in 2021 and Loctite 422 in 2022~~) or Araldite epoxy
resin (Araldite 2012).

Prey capture attempts were estimated from the transmitted head acceleration data obtained from the

accelerometer embedded in the CTD tags (referred to as “accelerometer processing,” as detailed in the SMRU Instrumentation manual 2023). The accelerometer mounted on this tag was initially configured to measure the three-axis acceleration at ~~a frequency of~~ 25 Hz. However, ~~owing due to limitations in~~ network bandwidth ~~limitations~~, summarized information was transmitted in lieu of complete acceleration data. To summarize prey capture behavior, the total jerk (m s^{-3}), ~~which is~~ the time derivative of acceleration, was calculated using the method outlined by Ydesen et al. (2014). For each second, the tag compared the maximum value of the root-mean-square (RMS) jerk to a threshold of 250 m s^{-3} to ascertain the occurrence of a prey capture attempt (PrCA) within that specific second. If the RMS jerk exceeded the threshold for several consecutive seconds, it was considered a single PrCA event. Due to bandwidth limitations, summarized information was transmitted by dividing dives into three phases (descent, bottom, and ascent) and indicating the phase in which PrCA occurred, instead of transmitting the exact time and depth. ~~The loggers divided each dive into three distinct segments. First, each~~ Each dive was fitted to 12 broken-stick points (i.e., the depth at the first point below the dive threshold (6 m), ~~10-ten~~ internal points, and the final point before the dive threshold (6 m)). The descent ~~segment-phase~~ commenced from the beginning of the dive and concluded at the first internal point, encompassing depths greater than 75% of the maximum depth. Similarly, the ascent ~~segment-phase was begun~~ began at the first internal point, where depths exceeded 75% of the maximum, and ending ~~at the conclusion of~~ after the dive. The ~~tags computed the~~ number of PrCA events for each ~~segment-phase was computed by the tags~~ and subsequently transmitted through a satellite network system.

2.2 Hydrological data

2.2.1 Quality control for hydrographic data

Temperature and salinity profiles obtained from seal-tagging observations were quality controlled ~~in accordance with~~ standard procedures widely used ~~for the low-resolution ascent profiles of in studies involving instrumented seals (Supplementary Fig. 12a; Boehme et al., 2009; Roquet et al., 2011; Siegelman et al. 2019 Yoon and Lee, 2021).~~ The procedure comprises three steps: ~~1- Tag-by-tag visualization; 2- pressure effect correction; 3- and~~ delayed mode calibration.

First, in Step 1, we checked reasonable ranges of temperature and salinity in Terra Nova Bay, Ross Sea, using historical (2014–2018) ship-based CTD data and ocean mooring (sourced from Yoon et al., 2020), and removed outliers from ~~both the 2021 and 2022, and 2023~~ seal-tagging data (Supplementary Fig. 12a). ~~Then~~ Subsequently, we applied the density removal algorithm regarding the minimum N^2 (N is the Brunt-Väisälä frequency) threshold as $1 \times 10^{-9} \text{ s}^{-2}$. ~~We also determined the density inversion depths at this step; Vertical profiles of N^2 show that the density removal algorithm was successfully applied to the three years of seal data the data at the density inversion depths were removed and filled with linear interpolation (Supplementary Figs. 12b, 12c, and 12d).~~ We found 500, ~~(1630), and 3333~~ irregular profiles out of the 3315, ~~(7552), and 7654~~ seal-tagging profiles recorded in 2021, ~~(2022), and 2023 respectively,~~ through Step 1 1; ~~therefore,~~ we used 2815, ~~(5922), and 4321~~ profiles from Step 2.

Second, in Step 2, we corrected the pressure effect for the temperature and salinity profiles using at-sea experimental data (Supplementary Fig. 2a; Roquet et al., 2011). The ~~at-sea experiment~~ in situ calibration constituted a ship-based calibration cast for CTD-SRDL sensors, ~~involving the attachment of~~ attaching CTD-SRDL sensors to the ~~ship's~~ CTD frame of the ship. Using at-sea experimental data, we derived linear relationships between temperature and salinity differences ~~between~~ for each CTD-SRDL sensor, and ship-based CTD data according to pressure (Roquet et al., 2011). Temperature and salinity biases were ~~then subsequently~~ removed from the entire profile of each tag according to the pressure calculated from each relationship (Roquet et al., 2011; ~~Yoon and Lee, 2021~~). The calibration cast was conducted only before the 2022 deployment; therefore, Step 2 was conducted only for the 2022 seal-tagging data.

Finally, in Step 3, we implemented a delayed-mode calibration approach to correct the offsets in the temperature and salinity profiles. Here, we used the High Salinity Shelf Water (HSSW) method (Supplementary Fig. 12 Yoon and Lee, 2021), as an alternative to the LCDW method generally used for correcting seal data in the Southern Ocean (Roquet et al., 2011) because LCDW is rarely found in the continental shelf region of the Ross Sea (Budillon et al., 2011), ~~and~~ HSSW, characterized by a homogeneous layer (Yoon et al., 2020), offers a ~~very~~

highly stable absolute reference for estimating offsets of seal-tagging data in Terra Nova Bay (TNB). Approximately one month after the 2021, 2022, and 2023 deployments, we conducted full-depth CTD casts at 56, 43, and 69 stations within Terra Nova Bay, Ross Sea, from December 6 to 25, 2020, (March 15–19, 2022, and December 3–17, 2023, respectively,) aboard the ice-breaking research vessel ARAON, respectively (Fig. 2 and Supplementary Fig. 23) (Fig. 2). Absolute values from ship-based CTD can be regarded as actual values because all CTD sensors of IBRV ARAON were sent to SeaBird Electronics (SBE; Manufacturer) for sensor calibration one year before the observation period. We corrected adjusted the offsets of the seal-tagging data by comparing the salinity and temperature of HSSW within the TNB observed from ship-based CTD profiles with those from seal-tagging profiles. Potential density over 28 kg m^{-3} and potential temperature below $-1.9 \text{ }^{\circ}\text{C}$ were used as criteria for HSSW (Yoon et al., 2020).

The salinity offset range for the 2021 seal data was from -0.16 to -0.03 , and the temperature was not adjusted because the temperature of HSSW from the 2021 seal data was consistent with those from the ship-based CTD data. Temperature and salinity offsets for 2022 seal data were estimated as $-0.03 \sim -0.23 \text{ }^{\circ}\text{C}$, and $-0.38 \sim -0.01$, respectively. Temperature and salinity offsets for 2023 seal data were estimated as $-0.01 \sim 0.27 \text{ }^{\circ}\text{C}$, and $-0.41 \sim -0.01$, respectively. As depicted in Figure 2 and Supplementary Fig. 23, the temperature and salinity of the quality-controlled seal tagging data-QC completed seal data show consistent features from demonstrated consistency with those derived from ship-based CTD data in Terra Nova Bay, Ross Sea.

Furthermore, we classified these water masses based on potential temperature and potential density to investigate the spatial and temporal variations in water masses within the continental shelf region of the Ross Sea, we classified these water masses based on potential temperature and potential density (Yoon et al., 2020). Potential temperature and potential density criteria for HSSW are defined as below $-1.9 \text{ }^{\circ}\text{C}$, and over 28 kg m^{-3} , respectively. Potential temperature and potential density for ice shelf water (ISW) are defined as below $-1.9 \text{ }^{\circ}\text{C}$, and below 28 kg m^{-3} , respectively. Modified shelf water (MSW) is defined as colder (warmer) than $-0.5 \text{ }^{\circ}\text{C}$ ($-1.9 \text{ }^{\circ}\text{C}$), and denser than 27.74 kg m^{-3} . For modified circumpolar deep water (MCDW), the potential temperature is defined as over $-0.5 \text{ }^{\circ}\text{C}$, and the potential density ranges between $27.74\text{--}27.88 \text{ kg m}^{-3}$. Antarctic surface water (AASW) is defined by temperatures colder than $-0.5 \text{ }^{\circ}\text{C}$ and densities lighter than 27.74 kg m^{-3} (Fig. 2a).

2.2.2 Kriging

A total of 8737–13,058 profiles were observed (2815, 5922, and 4321 in 2021, 2022, and 2023 respectively), and these were filtered through quality control procedures. To investigate the relationship between foraging behavior and the oceanographic environment, we calculated the physical characteristics of the water column at the maximum depth of each dive. Because the oceanographic and behavioral data obtained from the CTDs was not temporally matched, we employed the Kriging method, a commonly used technique for interpolating autocorrelated data, to calculate salinity and temperature because the oceanographic and behavioral data obtained from the CTDs did not temporally match (Oliver and Webster, 1990). Kriging was performed using the *gstat* package (Pebesma, 2004) in R, and the salinity and temperature at the maximum depth of each dive were obtained by calculating the two-dimensional space of depth and time. Water masses were classified based on these values. To account for the spatiotemporal anisotropy, we scaled the values between 0 and 1 based on the maximum and minimum values, and multiplied the time values by 50. Separate Kriging processes were conducted for the 2021, 2022, and 2023 datasets, and the reliability of the results was

confirmed via ~~5~~five-fold cross-validation. ~~The mean errors, root mean squared errors, and mean absolute errors for the kriging estimates are summarized in Supplementary Table 2. To create the~~ Hovmöller diagram (Fig. 3 a and b), salinity and temperature from 1 to 600 m-meter depth between February 15 and July 15 in 2022 were also calculated using kriging with seal-tagging profiles around Terra Nova Bay within the longitude range between 160 and 170°E and latitude range between 76 and 74°S.

~~The mean errors, root mean squared errors, and mean absolute errors were calculated (ME: < 0.0001 and 0.0012 for salinity and temperature, respectively, in 2021; < 0.0001 and 0.0022 for salinity and temperature, respectively, in 2022; 0.0004 and 0.0054 for salinity and temperature, respectively, in 2023; RMSE: 0.1107 and 0.1859 for salinity and temperature, respectively, in 2021; 0.1297 and 0.1496 for salinity and temperature, respectively, in 2022; 0.1883 and 0.1764 for salinity and temperature, respectively, in 2023; MAE: 0.0766 and 0.1131 for salinity and temperature, respectively, in 2021; 0.0891 and 0.0846 for salinity and temperature, respectively, in 2022; 0.1111 and 0.1073 for salinity and temperature, respectively, in 2023).~~

~~The mean errors, root mean squared errors, and mean absolute errors were calculated (ME < 0.001 for salinity and temperature in 2021 and 2022; RMSE: 0.1119 and 0.1816 for salinity and temperature, respectively, in 2021 and 0.1305 and 0.1477 for salinity and temperature, respectively, in 2022; MAE: 0.0766 and 0.1090 for salinity and temperature, respectively, in 2021 and 0.0897 and 0.0827 for salinity and temperature, respectively, in 2022).~~

2.4 Dive data classification and filtration

We distinguished between benthic and pelagic seal dives. The bathymetric depth corresponding to each dive location was assigned using bathymetry data from IBCSO (IBCSO.org, Dorschel et al., 2022). Dives characterized by a submergence depth of 80% or more of the assigned depth were classified as benthic dives (Kokubun et al., 2021). The Python package *pvl*ib (Holmgren et al., 2018) ~~was used to determine~~ d the solar altitude at each dive location and time, with altitudes above 0 ~~being~~ categorized as daytime and ~~altitudes~~ below 0 as nighttime. Dives with bathymetric values greater than 0 were excluded to eliminate inaccurately recorded dives. ~~When seal diving was deeper than the bathymetric values, the dives were~~ Dives that exceed bathymetry were remained and regarded as benthic dives due to uncertainty in the bathymetric data. Furthermore, dives with durations that were too short or long and depths that were too great (~~dive duration = 0 s, 0 <- dive duration <-> 5760 s, dive depth <-> 906 m~~; Heerah et al., 2013), ~~were also excluded. Dives and those~~ characterized by vertical travel speeds exceeding 5.1 m s⁻¹ were ~~also~~ excluded (Davis et al., 2003).

2.5 Statistics

To investigate the factors influencing the feeding behavior of Weddell seals, we set the response variable as log-transformed prey capture attempts (log(PCA_BTM + 1)) and used dive type (benthic or pelagic), season (month), sex, water mass, and year as explanatory variables to determine the minimal model through backward elimination. First, we compared the full model containing all explanatory variables against the models with each variable systematically removed using a likelihood test; through this process, we eliminated variables deemed non-contributory. After repeating this process, we obtained a parsimonious model containing only the important variables. Additionally, we compared all possible models created using different combinations of explanatory variables by comparing their Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values. ~~We subsequently and~~ obtained the best model with the smallest AIC and BIC values (Supplementary Tables ~~32~~ and ~~43~~). The explanatory variables of the best model obtained using the three methods (backward elimination, AIC, and BIC) were consistent. After finding the minimal model, we conducted post-hoc tests using the *multcomp* R package (Hothorn et al., 2008) to investigate differences in the categorical variables included in the minimal model (season and water mass). ~~We then tested whether~~ To examine diurnal patterns, we subsequently examined the effect of time periods on the dive depth, number of dives, and prey capture attempts ~~were determined by day and night to examine diurnal patterns.~~ Throughout this process, we created a linear mixed-effects model using the *nlme* R package (Pinheiro et al., 2022), in which we set each ~~individual~~ identity as a random effect and included a temporal autocorrelation term. ~~The models were run-estimated using restricted maximum likelihood (REML).~~ To ensure the robustness of our models, we performed Monte Carlo Cross Validation (CV) with a 4:1 train-test split and 100 iterations for each model. This approach allowed us to assess

[the stability and generalizability of the models. The standard deviations of the R-squared values were all below 0.02, further confirming the consistency and reliability of our models.](#)

295 3. Results

The telemetry data revealed that the Weddell seals in this study dispersed from the tagged region (near Jang Bogo Station; 62.2° S, 58.8° W) and traveled throughout continental shelf regions in the Ross Sea (Fig. 1). Among the ~~4864,7990~~14 dives observed, ~~911,192~~741 were categorized as benthic dives, ~~while and 3952,607~~273 were pelagic.

300 Seal CTD sensors have been used to observe five water masses in the continental shelf region of the Ross Sea: AASW, MCDW, MSW, ISW, and HSSW (Fig. 2; Orsi and Wiederwohl, 2009). When compared to the ship-based CTD data collected in the TNB during the austral summer of the same year, the seal tagging data showed a wider range of temperature and salinity of AASW (Fig. 2). The wide range of temperature and salinity values of the AASW represents its seasonal variation, being icy cold and fresh during the sea ice melting period (mainly austral summer), and subsequently transitioning to being warm and saline due to latent heat release and brine rejection during the sea ice formation period (mainly austral winter). The ~~lower boundary depth of the AASW exhibited a deepening trend~~ ~~27.8 kg /m³ isopycnal exhibited a shoaling trend~~ from ~~February~~mid-March onwards, eventually ~~aligning with the lower boundary depth of the MSW~~disappearing by salinity increase in the surface ~~due to brine rejection and vigorous mixing through the whole water column~~ by May (Fig. 33). ~~After May, HSSW and MSW, which are colder than -1.7 °C and denser than 27.8 kg /m³, were mainly identified in the TNB (Fig. 3).~~ These results support the notion that our seal-tagging data captured the increase in the density of AASW over the period between austral summer and winter. ~~The dive depth seems to show a trend of~~shows an increasing trend from March to July as the water temperature decreased ~~and~~while salinity and density increased (Fig. 3-c).

315 ~~Moreover, the presence of MCDW was more discernable in the seal-tagging profiles compared to the ship-based CTD data obtained from the TNB, despite its limited occurrence (only 1205 7-depths of 138,737058 profiles) (Figs. 1 and 2; Supplementary Fig. 34). This prominence arises because of seals diving into the Drygalski and Joides troughs near the continental shelf break region (Supplementary Fig. 1). Among seal data, more profiles were obtained near the shelf break and the eastern part of continental shelf regions in 2021 and 2022 than those in 2023 (Fig. 1). Due to this difference in spatial sampling, MCDW was identified more clearly in 2021 and 2022 compared to 2023 (Fig. 2; Supplementary Fig. 34). Furthermore, the ISW observed across the continental shelf region of the Ross Sea demonstrates a wider salinity range than the ISW observed in the TNB (Fig. 2), consistent with previous studies (ex.) Budillon et al., 2011). In both 2021, 2022, and 2023, properties of HSSW were well detected (Fig. 2) and it was mainly observed in the western part of the continental shelf region of the Ross Sea (Fig. 2; Supplementary Fig. 1) where polynyas exist (Fig. 2; Supplementary Fig. 31). Moreover, the presence of MCDW was more discernable in the seal-tagging profiles compared to the ship-based CTD data obtained from the TNB, despite its limited occurrence (only 107 depths of 8,737 profiles) (Fig. 2; Supplementary Fig. 1). This prominence arises because of seals diving into the northwestern part of the continental shelf region of the Ross Sea (Drygalski and Joides troughs), where MCDW is known to flow in (Jendersie et al., 2018; Supplementary Fig. 1). Furthermore, the ISW observed across the continental shelf region of the Ross Sea demonstrates a wider salinity range than the ISW observed in the TNB. This expansion can be attributed to the influence of ISW sourced from the McMurdo and Ross Ice Shelves (Fig. 2) (Budillon et al., 2011). In both 2021 and 2022, HSSW were mainly observed in the western part of the continental shelf region of the Ross Sea (Supplementary Fig. 1), proving that HSSW formed in the polynyas of the continental shelf region flows to the continental shelf break region along the Victoria Land (Silvano et al., 2020).~~

335 ~~In all three years, F~~the Weddell seals tagged in this study exhibited distinct diving behaviors across months. Figure 4 and Figure 5-a) illustrates the seasonal changes in dive depth. The dive depth ~~seems to show a trend of~~shows an increasing trend from March to July, whereas the number of PrCA events ~~appears to decrease~~decreases in June and July compared to March and April. When considering diving depth ($p < 0.001$; log likelihood ratio test between the best model and a model excluding the variable "season"), the shallowest dives

340 were undertaken in April, whereas the deepest diving occurred in July (197.200 ± 1347 m in April, 27065 ± 1584
m in July; mean \pm standard deviation) (Fig. 3; Tables 1, and 23). In terms of PrCA ($p < 0.001$; log likelihood ratio
test between the best model and a model excluding the variable “season”), the highest number was observed in
April, whereas the lowest occurred in June ($3.4829 \pm 5.246.11$ in April, $2.431.56 \pm 3.772.59$ in June) (Fig. 4(a);
345 Tables 32 and 4). Additionally, PrCA values varied based on water mass and dive type (benthic or pelagic) ($p <$
 0.001 for both; log likelihood ratio test between the best model and a model excluding the variables “water mass”
and “dive type”) despite the relative proportion of benthic dives not being predominant ($9192.11,741$ out of a
total of $48799.64,014$ dives, Fig. 4(c)). Based on our water mass definition, Weddell Seals performed many dives
in MSW (776.7376%), and dives with a high number frequent observations of PrCAs were also frequently
350 observed in MSW. The kernel density plots of distribution of dives on a TS-diagram are shown
in Supplementary Fig. 43. Notably, Weddell seals displayed a higher number of PrCA events in HSSW, MSW,
and ISW compared to AASW (an additional $1.14, 0.241.920.66$, and $0.220.750.65$ in PrCA per dive for HSSW,
MSW and ISW, respectively, compared to AASW). Conversely, there were no significant differences between
HSSW and the other water masses (Tables 2 and 5). Our seals had $0.22.860.58$ more PrCA ($p < 0.001$) during
benthic dives than in during pelagic dives (Fig. 4(b); Table 2).

355 Weddell seals demonstrated different diving behaviors between daytime and nighttime, delineated by
solar altitude. During daylight hours, seals dived an average of 796.84 m deeper and had a higher proportion of
benthic dives compared to nighttime (Figs. 5(a) and 5(d), Table 6). Additionally, seals demonstrated higher
foraging activity during the daytime, with an average of 24.9789 foraging attempts per dive, compared to 2.123
360 attempts during the nighttime (Fig. 5(b); Table 6). Interestingly, there was no discernible difference was
observed in the number of dives between the day and night (Fig. 5(c); Table 6).

4. Discussion

In this study, we observed a distinct seasonal pattern and water mass preference in the diving-foraging behavior
of Weddell seals: shallower dives were observed in April and July, respectively. Additionally, foraging frequencies were the highest in April and
365 observed in April and July, respectively. Additionally, foraging frequencies were the highest in April and
lowest in June. The detected water masses in the attached from the seal-CTD were MCDW, MSW, ISW, AASW,
and HSSW (Fig. 2; Supplementary Fig. 34). Among these, Weddell seals exhibited a preference for MSW and ISW
over AASW as their foraging habitats. In contrast, MCDW was rarely detected, and no significant preference
differences were found between HSSW and the other water masses concerning foraging activity. Furthermore, a
370 higher number of more PrCA events was were observed during benthic dives than those in contrast to pelagic
dives. Finally, a diel diving pattern among the seals was observed, with an increase in the proportion of benthic
dives, foraging frequency, diving depths, and the number of dives during the day compared to night. Finally, a diel
diving pattern among the seals was observed, with variations in the proportion of benthic dives, foraging
frequencies, and diving depths between day and night.

375 Concurrently recording external conditions is a commonly used approach to understand how marine
animals respond to their surrounding marine environment, it is a commonly used approach to concurrently
record external conditions. To best our knowledge, this is the first to measure the prey capture attempts of
Weddell seals in winter season directly using head acceleration with CTDerometers. Previous studies on Weddell
seals have often used CTD sensors to investigate water mass and foraging behavior. However, in those previous
380 studies, however, estimated foraging behaviors were inferred from indirect information, including horizontal
location, vertical swim speed, dive time, and dive depth rather than being directly measured (Goetz et al., 2023;
Nachtshiem et al., 2019; Kokubun et al., 2021; Goetz et al., 2023). While these proxies are indirect indices and
should be interpreted cautiously, acceleration data is particularly beneficial as it can directly detect PrCA,
providing a more accurate measure of foraging activity (Heerah et al., 2019; Allegue et al. 2023). The loggers
385 attached to our seals have acceleration sensors and CTD sensors. By directly measuring 3D head acceleration
with CTD, we could obtain more precise reliable data on the seals' foraging activities of the seals. This allows
us to correlate foraging activities with the recorded environmental conditions, providing a clearer understanding
of how these animals interact with their habitats. We think presume that the combination of CTD and

390 acceleration data offers a comprehensive view of both the physical environment and the behavioral responses of the seals, leading to more accurate and insightful conclusions.

Our results conclusively illustrate ~~that~~ a seasonal shift ~~exists~~ in diving depth and the number of PrCAs per dive. This phenomenon can be attributed to fluctuations in oceanographic and light conditions. Notably, Weddell seals ~~preferred~~ ~~exhibited a preference for~~ MSW or ISW over AASW during their foraging dives. As the lower boundary of the AASW shifted downward during June and July, ~~it is plausible that~~ the seals engaged in progressively deeper dives during the winter months possibly to follow the MSW or ISW. Secondly, a seasonal decrease in sunlight could limit prey accessibility, particularly pelagic fish species. The number of daylight hours in this region significantly decreased from March to July. ~~Based on data from Jang Bogo Station, on 1-March 1,~~ the duration of daylight duration was is over 16 h with a meridian altitude of over 23° ~~(based on data fromat Jang Bogo Station); however,~~ but the onset of the Polar night in early May (5th May in 2021; 6th May in 2022; 6th May in 2023) ~~led to the sun remaining below the horizon, resulted in continuous darkness without sunrise.~~ In the Ross Sea, the euphotic zone, where sufficient light for photosynthesis is available, is situated at a depth of 34 ± 13 m in spring, 26 ± 9 m in summer (mean ± standard deviation), and within a range of 14–66 m (range) in winter (Fabiano et al., 1993; Smith et al., 2013; ~~Fabiano et al., 1993~~). Below the euphotic zone lies the dysphotic zone, where light is present; ~~however, it is insufficient but not sufficient for the process of~~ photosynthesis to occur. Based on the findings of Sipler and Connelly (2015), the dysphotic zone in the Ross Sea extends to a depth of 170 m. Notably, Antarctic silverfish and holopelagic prey in the Ross Sea are found at depths of 0–700 m (De Witt et al., 1990), and their prey abundance is high in the upper water layers (50–200 m, Mintenbeck, 2008). This implies that Antarctic silverfish may inhabit ~~within~~ the euphotic and ~~/or~~ dysphotic zones. Weddell seals have been reported to use light and other senses, including vibrissal sensations, for swimming, detecting, and catching prey (Wartzok ~~and Davis et al., 1992;~~ Davis et al., 2004). Therefore, when sunlight is available, Weddell seals employ a combination of visual and other sensory inputs to capture pelagic or cryopelagic prey. Conversely, when sunlight is ~~not available~~ unavailable, or benthic prey are target, they must rely solely ~~rely~~ on non-visual sensory inputs for effective foraging. The diminished light conditions experienced in June and July posed challenges for seals ~~to locate in~~ locating prey, thereby leading to a decrease in PrCA events per dive and an increase in diving depths during these months compared to March.

The seasonal changes in diving behavior likely reflect corresponding seasonal changes in the distribution or composition of prey. Previous studies analyzing the diet of Weddell seals in the Ross Sea through scat or stomach contents have highlighted Antarctic silverfish as the primary pelagic prey consumed by Weddell seals across all seasons (~~Dearborn et al., 1965; Plötz et al., 1991;~~ Burns et al., 1998; ~~Dearborn et al., 1965; Plötz et al., 1991;~~ Goetz et al., 2017). Therefore, the increased dive depth of Weddell seals may suggest that the distribution of Antarctic silverfish, their main prey, and only holopelagic fish in the Ross Sea shifts deeper as winter approaches. Although, the seasonal variations in the vertical distribution of Antarctic silverfish remain unknown, Antarctic krill (*Euphausia superba*), one of their primary food sources, may migrate to deeper waters during winter when the sea surface is covered with ice and food in the upper waters becomes scarce (Smidt et al., 2011; Meyer et al., 2017). This could imply that Antarctic silverfish may migrate to deeper waters as winter approaches. ~~It is recognized that a~~ As Antarctic silverfish mature, they tend to inhabit deeper waters (La Mesa and Eastman, 2012), suggesting a shift in the prey composition towards larger and deeper-dwelling adult Antarctic silverfish as winter approaches. Another plausible factor behind this seasonal shift in diving behavior could be a corresponding shift in dietary preferences, involving greater consumption of benthic fish ~~compared to~~ than pelagic or cryopelagic fish. Additionally, seasonal variations in interspecific competition, particularly involving emperor penguins, another apex predator species in the Ross Sea year-round (~~Burns and Kooyman, 2001;~~ Smith et al., 2012; ~~Burns and Kooyman, 2015~~), could affect the foraging behavior of Weddell seals. In winter, emperor penguins must actively seek sustenance to nurture their offspring, ~~a necessity that~~ potentially ~~intensifies~~ intensifying interspecific competition with Weddell seals (Burns and Kooyman, 2001). Given that the diving capacity of emperor penguins is lower than that of adult Weddell seals (~~Kooyman et al., 1980;~~ Kooyman and Kooyman, 1995; ~~Kooyman et al., 1980;~~ Burns, 1999), Weddell seals may forage at greater depths to minimize interspecific competition. _

There was in a previous study on Weddell seals in the Ross Sea showed that, seasonal changes in foraging behavior were observed, with dive depth increasing and foraging activity intensifying from summer to

440 winter (Goetz et al., 2023). The seasonal increase of dive depth was in accordance with agreed with our finding, but the findings; however, their foraging results showed the opposite compared to contrary of our results. In Goetz et al. (2023's study from 2010 to 2012) observed that, foraging of seals was the highest in winter of 2010 to 2012. However, We do not have the supporting evidence to explain the difference. This could be due to the different seasonal prey availability in the Ross Sea between the two studies. In the Ross Sea ecosystem, the diet composition of Weddell seals are known to exhibit considerable interannual variability (Goetz et al., 2017). The sea ice extent and the food availability in the Ross Sea for top predators can vary annually (Ainley et al., 2020), and s. There is a possibility that s Such variations in sea ice extent can possibly influence plankton blooms and the seasonal prey abundance composition which in turn influence the entire food chain, including higher trophic levels such as krills, fish, and seals for seals between the two studies (Arrigo et al., 2004; Lorrain et al., 2009). Otherwise, Despite the consistency in dive depth, the differences in foraging activity are thought to could be owing to result from be due to the different methods used measurements to infer foraging efforts. Since The results in winter foraging could be overestimated because the previous study used an indirect estimation (a track-driven metric) for foraging activity was inferred using a track-driven metric, and the results in winter foraging could be over-estimated may reflect seasonal changes in factors other than foraging. The track-driven metric estimation is based on the assumption that all behaviors involving movement within a certain radius are associated with area-restricted search (ARS). However, behaviors other than foraging or movement (e.g., sleeping, resting) could also be regarded as ARS. Goetz et al. excluded haul-out periods from the FPT analysis to address this possibility. Nevertheless, haul-out times significantly decrease in winter while dive times increase (Boehme et al., 2016). This increase in dives during winter might suggest that the dives could be for purposes other than foraging, such as resting or sleeping. The First Passage Time method used in previous study (Goetz et al. 2023) assumes that all behaviors involving movement within a certain radius are associated with Area-Restricted Search (ARS). However, behaviors other than foraging or movement (e.g., sleeping, resting) could also be regarded as ARS. To resolve this issue, Goetz et al. excluded haul-out periods from the FPT analysis. However, in winter, haul-out times significantly decrease while dive times increase (Boehme et al. 2016). The increased dives during winter could lead to such differences if the dives are for purposes other than foraging, such as resting or sleeping.

Our seal CTD data revealed a dynamic alteration in the vertical distribution of water masses changes in vertical stratification in accordance with by the seasons. During early austral fall, the water columns within the Ross Sea are clearly structured, with HSSW, MSW, and AASW from the bottom up; however, this stratification weakens as winter advances; strong mixing owing to the influence of winds coupled with active sea ice formation at the surface serve to diminishes the stratification over the whole water column density difference between AASW and shelf water, effectively erasing their distinct boundaries (Figs. 3b and 3c). Additionally, ISW exists near the ice shelves instead of spreading out to the central part of the continental shelf region (Supplementary Fig. 31). This behavior might be associated with the relatively lower rates of basal melt and meltwater flux of ice shelves in the Ross Sea (Supplemetnary Fig. 1; Rignot et al., 2013; Rignot et al., 2019).

Weddell seals exhibited more frequent feeding behavior in HSSW, MSW, and ISW than in compared to AASW AASW, and they rarely ventured into MCDW. These findings might reflect the inherent nutrient composition of each water mass. HSSW is the densest water mass (potential density > 28 kg m⁻³) in the Ross Sea in the Ross Sea and is primarily formed by coastal polynya activity in the Ross Sea (Budillon et al., 2011; Yoon et al., 2020), and the In coastal polynyas, not only is dense shelf water formed, but the products of biological products from the surface ion areare being also transported to depth, reducing surface nutrients and increasing accumulating nutrient contents of HSSW at depth (Arrigo et al., 2008; DeJong et al., 2017; Ingrassio et al., 2022). For benthic fish, it provides unique habitats that are critical for benthic fish for the survival and distribution (La Mesa et al., 2004). In our results, dives in HSSW were mostly performed in the benthic (69.4%). Thus, HSSW may contain prey, usually benthic species, for seals. –

MSW is formed through the by mixing of shelf water with surrounding water masses, including MCDW, within the continental shelf region. –MCDW plays a is crucial role in heat and nutrient cycling in the Southern Ocean because it is warm and nutrient-rich (Smith et al., 2012; Kutska et al., 2015; Gerringa et al., 2020). MCDW contain contains a significantly higher concentration of macro-nutrients and also contributes to the basal melt of ice shelves, which may in turn increase primary production. However, the dissolved oxygen (DO) levels in

MCDW are notably low, falling below 5 mL L^{-1} mL/L (Jenkins et al., 2018; Yoon et al., 2020). This is lower than the critical threshold of oxygen concentration for krill, implying that the prey availability for seals in MCDW would be limited (Brierley and Coxet al., 2010; Kils, 1979). However, MSW may contain a high amount of nutrients from MCDW and sufficient oxygen contents (Orsi and Wiederwohl, 2009; Smith et al., 2014, 2021). According to ship-based CTD observations with SBE43 DO sensor values in TNB during the austral summer 2021 and 2022, and 2023, it was found that the DO of MSW was over 6.5 mL L^{-1} mL/L .

ISW is a water mass formed by the melting of ice shelves and is characterized by a potential temperature below the freezing point. This water mass can harbor essential nutrients, such as iron, which may be present on ice shelves; thus, potentially making ISW a nutrient source (Sedwick and DiTullio, 1997; Smith et al., 2014). Nutrient-rich hydrographic conditions may be related to the high prey availability. In other regions, Weddell seals exhibit increased foraging behavior under nutrient-rich conditions in other regions (Heerah et al., 2013; Nachtsheim et al., 2019; Kokubun et al., 2021). Moreover, ISW also has relatively higher oxygen, for example, DO sensor values of ISW in TNB during the austral summer of 2021, 2022 and 2023 are higher than 6.4 mL L^{-1} . AASW is generally deficient in nutrients by vigorous biological processes despite the high DO. Therefore, Weddell seals could have a higher number of PrCA events in MSW and ISW than AASW and MCDW because they satisfy both rich nutrients and high-DO characteristics. HSSW is a water mass present in the lowest part of the water column in the Ross Sea and is associated with the benthic community. A notable portion of the Weddell seal's diet is known to consist of benthic prey (Davis et al., 2004; Goetz et al., 2017), which aligns with findings that Weddell seals exhibit more feeding activity in HSSW compared to AASW.

Although only 18.8% of all dives were categorized as benthic dives, a greater number of more foraging attempts were observed during these dives. This higher foraging attempts near the bottom are consistent with a previous study in the Ross Sea (Goetz et al., 2023). From an energy-efficiency perspective, the costs associated with the diving behavior of Weddell seals increase as the duration of their dives increases. In particular, dives lasting longer than 23 min entail additional anaerobic costs. Despite the substantial energetic costs associated with prolonged dives, the benthic zone serves as a habitat for numerous sizeable prey species weighing over 1 kg, including the Antarctic toothfish and icefish (La Mesa, 2004; Goetz et al., 2017). Hence, Weddell seals can reap substantial benefits in the benthic zone. This dynamic could result in a higher frequency of foraging attempts per dive during benthic dives compared to than pelagic dives for larger prey. However, only 18.8% of all dives were categorized as benthic dives. This high foraging attempts at the bottom result is consistent with a previous study in the Ross Sea (Goetz et al., 2023) that inferred foraging behavior in the Ross Sea using first passage time (FPT). In that study, Weddell seals exhibited high FPT at the bottom of the water column throughout the year. Furthermore, PrCA instances were estimated by tallying the occurrences of jerks (the temporal derivatives of acceleration) surpassing the predefined threshold (250 m s^{-3}), as recorded on the bio-logger attached to the head of the Weddell seal. Benthic prey in the Ross Sea predominantly comprises hefty fish, such as Icefish or Antarctic toothfish, and other fish that are heavier than the Antarctic silverfish, the only holopelagic fish in the Ross Sea whose adult form exceeds 50g. Diving predators require increased mobility to effectively handle larger prey, resulting in higher variance in behavioral data, including acceleration (Watanabe and Takahashi, 2013; Volpov et al., 2015; Watanabe and Takahashi, 2013). Weddell seals also handle large prey such as Antarctic toothfish, the flesh part of which are is exclusively consumed by them (Davis et al., 2004; Ainley and Sniff, 2009; Davis et al., 2004; Goetz et al., 2017). Therefore, this study acknowledges the likelihood that foraging frequency may have been overestimated during the instances when Weddell seals handling handle larger prey.

Differences in diving behavior between the day and night were also observed. Although the total number of dives did not differ between the day and night, Weddell seals performed deeper dives during the day, which was marked by a higher incidence of benthic dives and PrCA events; however, no significant differences between the time periods were observed. The variation in diel patterns of diving depth could potentially be attributed to the vertical migration behavior of pelagic prey. This migration phenomenon is well-documented among pelagic fish species, including Antarctic pelagic fish, which exhibit a diel vertical migration pattern. Such This fish dive to greater depths as the amount of light at the surface increases, effectively reducing their vulnerability to visual predators that rely on light to locate and pursue prey (Childress, 1995; Fuiman et al., 2002; Hays, 2003; Robison, 2003; Sutton, 2013). Weddell Moreover, seals also rely on their visual senses to detect prey

(Davis et al., 1999). Thus, these seals can dive to greater depths during the day, corresponding to the migratory behavior of pelagic prey in the Ross Sea. Additionally, the energy expenditure associated with hunting pelagic prey may increase with deeper dives during the day, ~~whereas. In contrast,~~ the cost of hunting benthic prey may decrease as ~~the amount of~~ light increases. Therefore, the proportion of benthic dives ~~is inclined to rise~~ increases during the day. As visual predators, Weddell seals are ~~better equipped to seek and pursue prey in the more adept at hunting during~~ daytime, ~~compared to nighttime, when their senses other than sight are~~ predominantly employed on their vision. Consequently, the number of PrCA events increased during the daylight hours.

5. Conclusion

Concurrently analyzing hydrographic and behavioral data from the Ross Sea revealed seasonal variations in the foraging behavior of Weddell seals, ~~which was~~ closely linked to shifts in oceanographic environmental conditions (Fig. 6; ~~Supplementary Fig. 5~~). The seals demonstrated a preference for water masses, which could potentially be both nutrient-rich and high-DO, and exhibited distinct foraging strategies depending on the light conditions during the day and night. This study demonstrates that Weddell seals adjust their foraging behavior, ~~adapting both~~ spatially and temporally ~~in response to~~ adapting environmental factors. Over the last several decades, the hydrography of the Ross Sea has undergone considerable changes with an increasingly warming world (Castagno et al., 2019; ~~Yoon et al., 2020~~; Silvano et al., 2020; Thomas et al., 2020; ~~Yoon et al., 2020~~). This suggests a continuous ~~process of~~ adaptation ~~process~~ in the foraging behaviors of marine mammals, including Weddell seals, as they navigate changing marine environments. Therefore, ~~it is necessary to continuously monitor~~ continuous monitoring of the foraging behavior of marine mammals in the Ross Sea ~~is necessary~~. Our findings serve as a baseline and establish a foundational understanding for future research, particularly concerning the impact of marine environmental changes on the ecosystem of the Ross Sea MPA.

Data Availability

The behavioral and oceanographic data related to this study can be accessed at the Korea Polar Data Center (KPDC) website, kpsc.kopri.re.kr. The datasets are available under the following DOIs:

- <https://dx.doi.org/doi:10.22663/KOPRI-KPDC-00002402.1>

- <https://dx.doi.org/doi:10.22663/KOPRI-KPDC-00002401.1>

- <https://dx.doi.org/doi:10.22663/KOPRI-KPDC-00002077.1>

- <https://dx.doi.org/doi:10.22663/KOPRI-KPDC-00001658.4>

Author Contributions

~~HC, S-TY and WYL designed the research and all authors contributed to the conceptualization. JP conducted the investigation in 2020. MP, YK and UC conducted the investigation in 2021. WY and JSN conducted the investigation in 2023. HAC and S-TY performed the quality control of raw data for formal analysis. SY and WSL participated the methodology and project administration. HC did the data curation and contributed to formal analysis. HC, S-TY, and WYL prepared the original draft manuscript and revised it with comments from all authors. This part will be filled out before submission.~~

Competing Interests

The authors declare no competing interests.

Acknowledgements

This work was supported by ~~a~~ Korea Polar Research Institute (KOPRI) grant funded by the Ministry of Oceans and Fisheries (KOPRI ~~PE21140, 22140,~~ PE23140; WYL, JP, HC, MJP, YK, and UC) and supported by ~~the~~ Korea Institute of Marine Science & Technology Promotion (KIMST) funded by the Ministry of Oceans and Fisheries (RS-2023-00256677; PM23020; WYL, HC, ~~JK,~~ SY, WSL, ~~HAC, JSN,~~ and S-TY). This research was also supported by Basic Science Research Program through National Research Foundation of Korea (NRF) funded by the Ministry of Education (2022R111A3063629; S-TY, ~~and HAC~~).

References

- Ainley, D. G. and Siniff, D. B.: The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea, *Antarct Sci*, 21, 317, <https://doi.org/10.1017/S0954102009001953>, 2009.
- 595 Ainley, D. G., Larue, M. A., Stirling, I., Stammerjohn, S., and Siniff, D. B.: An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast, *Mar Mamm Sci*, 31, 1338–1361, <https://doi.org/10.1111/mms.12220>, 2015.
- 600 [Ainley, D. G., Joyce, T. W., Saenz, B., Pitman, R. L., Durban, J. W., Ballard, G., Daly, K., and Kim, S.: Foraging patterns of Antarctic minke whales in McMurdo Sound, Ross Sea, *Antarctic Science*, 32, 454–465, <https://doi.org/10.1017/S0954102020000310>, 2020.](https://doi.org/10.1017/S0954102020000310)
- [Allegue, H., Réale, D., Picard, B., and Guinet, C.: Track and dive-based movement metrics do not predict the number of prey encountered by a marine predator, *Mov Ecol*, 11, 3, <https://doi.org/10.1186/s40462-022-00361-2>, 2023.](https://doi.org/10.1186/s40462-022-00361-2)
- 605 Arce, F., Hindell, M. A., McMahon, C. R., Wotherspoon, S. J., Guinet, C., Harcourt, R. G., and Bestley, S.: Elephant seal foraging success is enhanced in Antarctic coastal polynyas, *Proceedings of the Royal Society B*, 289, <https://doi.org/10.1098/RSPB.2021.2452>, 2022.
- [Arrigo, K. R., van Dijken, G. L., and Bushinsky, S.: Primary production in the Southern Ocean, 1997–2006, *Journal of Geophysical Research: Oceans*, 113, 8004, <https://doi.org/10.1029/2007JC004551>, 2008.](https://doi.org/10.1029/2007JC004551)
- 610 Aubone, N., Saraceno, M., Torres Alberto, M. L., Campagna, J., Ster, L. Le, Picard, B., Hindell, M., Campagna, C., and Guinet, C. R.: Physical changes recorded by a deep diving seal on the Patagonian slope drive large ecological changes, *Journal of Marine Systems*, 223, 103612, <https://doi.org/10.1016/j.jmarsys.2021.103612>, 2021.
- Bailleul, F., Charrassin, J. B., Ezraty, R., Girard-Ardhuin, F., McMahon, C. R., Field, I. C., and Guinet, C.: Southern elephant seals from Kerguelen Islands confronted by Antarctic Sea ice. Changes in movements and in diving behaviour, *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 343–355, <https://doi.org/10.1016/J.DSR2.2006.11.005>, 2007.
- 615 Boehme, L., Lovell, P., Biuw, M., Roquet, F., Nicholson, J., Thorpe, S. E., Meredith, M. P., and Fedak, M.: Technical Note: Animal-borne CTD-Satellite Relay Data Loggers for real-time oceanographic data collection, *Ocean Science*, 5, 685–695, <https://doi.org/10.5194/os-5-685-2009>, 2009.
- 620 [Boehme, L., Baker, A., Fedak, M., Årthun, M., Nicholls, K., Robinson, P., Costa, D., Biuw, M., and Photopoulou, T.: Bimodal Winter Haul-Out Patterns of Adult Weddell Seals \(*Leptonychotes weddellii*\) in the Southern Weddell Sea, *PLOS ONE*, 11, e0155817, <https://doi.org/10.1371/journal.pone.0155817>, 2016.](https://doi.org/10.1371/journal.pone.0155817)
- [Brierley, A. S. and Cox, M. J.: Shapes of Krill Swarms and Fish Schools Emerge as Aggregation Members Avoid Predators and Access Oxygen, *Current Biology*, 20, 1758–1762, <https://doi.org/10.1016/j.cub.2010.08.041>, 2010.](https://doi.org/10.1016/j.cub.2010.08.041)
- 625 Brooks, C. M., Bloom, E., Kavanagh, A., Nocito, E. S., Watters, G. M., and Weller, J.: The Ross Sea, Antarctica: A highly protected MPA in international waters, *Mar Policy*, 134, 104795, <https://doi.org/10.1016/j.marpol.2021.104795>, 2021.
- Budillon, G., Castagno, P., Aliani, S., Spezie, G., and Padman, L.: Thermohaline variability and Antarctic bottom water formation at the Ross Sea shelf break, *Deep Sea Research Part I: Oceanographic Research Papers*, 58, 1002–1018, <https://doi.org/10.1016/J.DSR.2011.07.002>, 2011.
- 630 Burns, J. M.: The development of diving behavior in juvenile Weddell seals: pushing physiological limits in order to survive, *Can J Zool*, 77, 737–747, <https://doi.org/10.1139/z99-022>, 1999.

- Burns, J. M. and Kooyman, G. L.: Habitat Use by Weddell Seals and Emperor Penguins Foraging in the Ross Sea, Antarctica, *Am Zool*, 41, 90–98, <https://doi.org/10.1093/icb/41.1.90>, 2001.
- 635 Burns, J. M., Trumble, S. J., Castellini, M. A., and Testa, J. W.: The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis, *Polar Biol*, 19, 272–282, <https://doi.org/10.1007/S003000050245/METRICS>, 1998.
- Castagno, P., Capozzi, V., DiTullio, G. R., Falco, P., Fusco, G., Rintoul, S. R., Spezie, G., and Budillon, G.: Rebound of shelf water salinity in the Ross Sea, *Nat Commun*, 10, 5441, <https://doi.org/10.1038/s41467-019-13083-8>, 2019.
- 640 Childress, J. J.: Are there physiological and biochemical adaptations of metabolism in deep-sea animals?, *Trends Ecol Evol*, 10, 30–36, [https://doi.org/10.1016/S0169-5347\(00\)88957-0](https://doi.org/10.1016/S0169-5347(00)88957-0), 1995.
- ~~Collins, K. T., Terhune, J. M., Rogers, T. L., Wheatley, K. E., and Harcourt, R. G.: Vocal individuality of in-air Weddell seal (*Leptonychotes weddellii*) pup “primary” calls, *Mar Mamm Sci*, 22, 933–951, <https://doi.org/10.1111/j.1748-7692.2006.00074.x>, 2006.~~
- 645 Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S., and Horning, M.: Hunting Behavior of a Marine Mammal Beneath the Antarctic Fast Ice, *Science* (1979), 283, 993–996, <https://doi.org/10.1126/science.283.5404.993>, 1999.
- Davis, R. W., Fuiman, L. A., Williams, T. M., Horning, M., and Hagey, W.: Classification of Weddell seal dives based on 3 dimensional movements and video-recorded observations, *Mar Ecol Prog Ser*, 264, 109–122, <https://doi.org/10.3354/MEPS264109>, 2003.
- 650 Davis, R. W., Hagey, W., and Horning, M.: Monitoring the behavior and multi-dimensional movements of Weddell seals using an animal-borne video and data recorder, *Memoirs of National Institute of Polar Research. Special issue*, 58, 148–154, 2004.
- Dearborn, J. H.: Food of Weddell Seals at McMurdo Sound, Antarctica, *J Mammal*, 46, 37, <https://doi.org/10.2307/1377814>, 1965.
- ~~DeJong, H. B., Dunbar, R. B., Koweek, D. A., Mucciarone, D. A., Bercovici, S. K., and Hansell, D. A.: Net community production and carbon export during the late summer in the Ross Sea, Antarctica, *Global Biogeochemical Cycles*, 31, 473–491, <https://doi.org/10.1002/2016GB005417>, 2017.~~
- 660 DeWitt, H. H., Heemstra, P. C., and Gon, O.: Nototheniidae, in: *Fishes of the Southern Ocean*, edited by: Heemstra, P. C. and Gon, O., JLB Smith Institute of Ichthyology, Grahamstown, 279–331, 1990.
- Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., and Talley, L. D.: Climate Change Impacts on Marine Ecosystems, <https://doi.org/10.1146/annurev-marine-041911-111611>, 4, 11–37, <https://doi.org/10.1146/ANNUREV-MARINE-041911-111611>, 2011.
- 665 Dorschel, B., Hehemann, L., Viquerat, S., Warnke, F., Dreutter, S., Tenberge, Y. S., Accettella, D., An, L., Barrios, F., Bazhenova, E., Black, J., Bohoyo, F., Davey, C., De Santis, L., Dotti, C. E., Fremand, A. C., Fretwell, P. T., Gales, J. A., Gao, J., Gasperini, L., Greenbaum, J. S., Jencks, J. H., Hogan, K., Hong, J. K., Jakobsson, M., Jensen, L., Kool, J., Larin, S., Larter, R. D., Leitchenkov, G., Loubrieu, B., Mackay, K., Mayer, L., Millan, R., Morlighem, M., Navidad, F., Nitsche, F. O., Nogi, Y., Pertuisot, C., Post, A. L., Pritchard, H. D., Purser, A., Rebesco, M., Rignot, E., Roberts, J. L., Rovere, M., Ryzhov, I., Sauli, C., Schmitt, T., Silvano, A., Smith, J., Snaith, H., Tate, A. J., Tinto, K., Vandenbossche, P., Weatherall, P., Wintersteller, P., Yang, C., Zhang, T., and Arndt, J. E.: The International Bathymetric Chart of the Southern Ocean Version 2, *Sci Data*, 9, 275, <https://doi.org/10.1038/s41597-022-01366-7>, 2022.
- 675 ~~Fabiano, M., Povero, P., and Danovaro, R.: Distribution and composition of particulate organic matter in the Ross Sea (Antarctica), *Polar Biol*, 13, 525–533, <https://doi.org/10.1007/BF00236394>, 1993. Fabiano, M., Povero, P., and Danovaro, R.: Distribution and composition of particulate organic matter in the Ross Sea (Antarctica), *Polar Biol*,~~

~~13, 525–533, <https://doi.org/10.1007/BF00236394>/METRICS, 1993.~~

Fuiman, L. A., Davis, R. W., and Williams, T. M.: Behavior of midwater fishes under the Antarctic ice: observations by a predator, *Marine Biology* 2002 140:4, 140, 815–822, <https://doi.org/10.1007/S00227-001-0752-Y>, 2002.

680 [Gerringa, L. J. A., Alderkamp, A. C., van Dijken, G., Laan, P., Middag, R., and Arrigo, K. R.: Dissolved Trace Metals in the Ross Sea, *Frontiers in Marine Science*, 7, 577098, <https://doi.org/10.3389/fmars.2020.577098>, 2020.](#)

Goetz, K. T., Burns, J. M., Hückstädt, L. A., Shero, M. R., and Costa, D. P.: Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea, *Deep Sea Research Part II: Topical Studies in Oceanography*, 140, 36–44, <https://doi.org/10.1016/j.dsr2.2016.05.017>, 2017.

685 Goetz, K. T., Dinniman, M. S., Hückstädt, L. A., Robinson, P. W., Shero, M. R., Burns, J. M., Hofmann, E. E., Stammerjohn, S. E., Hazen, E. L., Ainley, D. G., and Costa, D. P.: Seasonal habitat preference and foraging behaviour of post-moult Weddell seals in the western Ross Sea, *R Soc Open Sci*, 10, <https://doi.org/10.1098/rsos.220500>, 2023.

690 [Harcourt, R. G., Kingston, J. J., Waas, J. R., and Hindell, M. A.: Foraging while breeding: alternative mating strategies by male Weddell seals?, *Aquat Conserv*, 17, S68–S78, <https://doi.org/10.1002/AQC.915>, 2007.](#)

Harcourt, R. G., Hindell, M. A., McMahon, C. R., Goetz, K. T., Charrassin, J.-B., Heerah, K., Holser, R., Jonsen, I. D., Shero, M. R., Hoenner, X., Foster, R., Lenting, B., Tarsisz, E., and Pinkerton, M. H.: Regional Variation in Winter Foraging Strategies by Weddell Seals in Eastern Antarctica and the Ross Sea, *Front Mar Sci*, 8, 0–13, <https://doi.org/10.3389/fmars.2021.720335>, 2021.

695 ~~Harcourt, R. G., Kingston, J. J., Waas, J. R., and Hindell, M. A.: Foraging while breeding: alternative mating strategies by male Weddell seals?, *Aquat Conserv*, 17, S68–S78, <https://doi.org/10.1002/AQC.915>, 2007.~~

Hays, G. C.: A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations, *Hydrobiologia*, 503, 163–170, <https://doi.org/10.1023/B:HYDR.0000008476.23617.b0>~~<https://doi.org/10.1023/B:HYDR.0000008476.23617.B0/METRICS>~~, 2003.

700 Heerah, K., Andrews-Goff, V., Williams, G., Sultan, E., Hindell, M., Patterson, T., and Charrassin, J.-B.: Ecology of Weddell seals during winter: Influence of environmental parameters on their foraging behaviour, *Deep Sea Research Part II: Topical Studies in Oceanography*, 88–89, 23–33, <https://doi.org/10.1016/j.dsr2.2012.08.025>, 2013.

705 Heerah, K., Cox, S. L., Blevin, P., Guinet, C., and Charrassin, J.-B.: Validation of Dive Foraging Indices Using Archived and Transmitted Acceleration Data: The Case of the Weddell Seal, *Front Ecol Evol*, 7, <https://doi.org/10.3389/fevo.2019.00030>, 2019.

Holmgren, W. F., Hansen, C. W., and Mikofski, M. A.: pviib python: a python package for modeling solar energy systems, <https://doi.org/10.21105/joss.00884>, 2018.

710 Hothorn, T., Bretz, F., and Westfall, P.: Simultaneous Inference in General Parametric Models, *Biometrical Journal*, 50, 346–363, <https://doi.org/10.1002/BIMJ.200810425>, 2008.

Huang, T., Sun, L., Stark, J., Wang, Y., Cheng, Z., Yang, Q., and Sun, S.: Relative Changes in Krill Abundance Inferred from Antarctic Fur Seal, *PLoS One*, 6, e27331, <https://doi.org/10.1371/journal.pone.0027331>, 2011.

715 Hückstädt, L. A., Piñones, A., Palacios, D. M., McDonald, B. I., Dinniman, M. S., Hofmann, E. E., Burns, J. M., Crocker, D. E., and Costa, D. P.: Projected shifts in the foraging habitat of crabeater seals along the Antarctic Peninsula, *Nat Clim Chang*, 10, 472–477, <https://doi.org/10.1038/s41558-020-0745-9>, 2020.

- [Ingrosso, G., Giani, M., Kralj, M., Comici, C., Rivaro, P., Budillon, G., Castagno, P., Zoccarato, L., and Celussi, M.: Physical and biological controls on anthropogenic CO₂ sink of the Ross Sea, *Front. Mar. Sci.*, **9**, <https://doi.org/10.3389/fmars.2022.954059>, 2022.](https://doi.org/10.3389/fmars.2022.954059)
- 720 Jacobs, S. S., Giulivi, C. F., and Mele, P. A.: Freshening of the Ross Sea During the Late 20th Century, *Science* (1979), **297**, 386–389, <https://doi.org/10.1126/science.1069574>, 2002.
- Jendersie, S., Williams, M. J. M., Langhorne, P. J., and Robertson, R.: The Density-Driven Winter Intensification of the Ross Sea Circulation, *J Geophys Res Oceans*, **123**, 7702–7724, <https://doi.org/10.1029/2018JC013965>, 2018.
- 725 [Jenkins, A., Shoosmith, D., Dutrieux, P., Jacobs, S., Kim, T. W., Lee, S. H., Ha, H. K., and Stammerjohn, S.: West Antarctic Ice Sheet retreat in the Amundsen Sea driven by decadal oceanic variability, *Nature Geosci*, **11**, 733–738, <https://doi.org/10.1038/s41561-018-0207-4>, 2018.](https://doi.org/10.1038/s41561-018-0207-4)
- Kokubun, N., Tanabe, Y., Hirano, D., Mensah, V., Tamura, T., Aoki, S., and Takahashi, A.: Shoreward intrusion of oceanic surface waters alters physical and biological ocean structures on the Antarctic continental shelf during winter: Observations from instrumented seals, *Limnol Oceanogr*, **66**, 3740–3753, <https://doi.org/10.1002/lno.11914>, 2021.
- 730 Kooyman, G. L. and Kooyman, T. G.: Diving Behavior of Emperor Penguins Nurturing Chicks at Coulman Island, Antarctica, *Condor*, **97**, 536–549, <https://doi.org/10.2307/1369039>, 1995.
- Kooyman, G. L., Wahrenbrock, E. A., Castellini, M. A., Davis, R. W., and Sinnett, E. E.: Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: Evidence of preferred pathways from blood chemistry and behavior, *Journal of Comparative Physiology ? B*, **138**, 335–346, <https://doi.org/10.1007/BF00691568>, 1980.
- 735 Kustka, A. B., Kohut, J. T., White, A. E., Lam, P. J., Milligan, A. J., Dinniman, M. S., Mack, S., Hunter, E., Hiscock, M. R., Smith, W. O., and Measures, C. I.: The roles of MCDW and deep water iron supply in sustaining a recurrent phytoplankton bloom on central Pennell Bank (Ross Sea), *Deep Sea Research Part I: Oceanographic Research Papers*, **105**, 171–185, <https://doi.org/10.1016/j.dsr.2015.08.012>, 2015.
- 740 Labrousse, S., Ryan, S., Roquet, F., Picard, B., McMahon, C. R., Harcourt, R., Hindell, M., Le Goff, H., Lourenco, A., David, Y., Sallée, J.-B. B., and Charrassin, J.-B. B.: Weddell seal behaviour during an exceptional oceanographic event in the Filchner-Ronne Ice Shelf in 2017, *Antarct Sci*, **33**, 252–264, <https://doi.org/10.1017/S0954102021000092>, 2021.
- 745 LaRue, M., Salas, L., Nur, N., Ainley, D., Stammerjohn, S., Pennycook, J., Dozier, M., Saints, J., Stamatiou, K., Barrington, L., and Rotella, J.: Insights from the first global population estimate of Weddell seals in Antarctica, *Sci Adv*, **7**, 3674–3698, <https://doi.org/10.1126/SCIADV.ABH3674>, 2021.
- [Lorrain, A., Graham, B., Ménard, F., Popp, B., Bouillon, S., Breugel, P. van, and Cherel, Y.: Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean, *Marine Ecology Progress Series*, **391**, 293–306, <https://doi.org/10.3354/meps08215>, 2009.](https://doi.org/10.3354/meps08215)
- 750 [McMahon, C. R., Roquet, F., Baudel, S., Belbeoch, M., Bestley, S., Blight, C., Boehme, L., Carse, F., Costa, D. P., Fedak, M. A., Guinet, C., Harcourt, R., Heslop, E., Hindell, M. A., Hoenner, X., Holland, K., Holland, M., Jaine, F. R. A., Jeanniard du Dot, T., Jonsen, I., Keates, T. R., Kovacs, K. M., Labrousse, S., Lovell, P., Lydersen, C., March, D., Mazloff, M., McKinzie, M. K., Muelbert, M. M. C., O'Brien, K., Phillips, L., Portela, E., Pye, J., Rintoul, S., Sato, K., Sequeira, A. M. M., Simmons, S. E., Tsonos, V. M., Turpin, V., van Wijk, E., Vo, D., Wege, M., Whoriskey, F. G., Wilson, K., and Woodward, B.: Animal-Borne Ocean Sensors—AniBOS—An Essential Component of the Global Ocean Observing System, *Front Mar Sci*, **8**, <https://doi.org/10.3389/fmars.2021.751840>, 2021.](https://doi.org/10.3389/fmars.2021.751840)
- 755 La Mesa, M. and Eastman, J. T.: Antarctic silverfish: life strategies of a key species in the high-Antarctic ecosystem, *Fish and Fisheries*, **13**, 241–266, <https://doi.org/10.1111/j.1467-2979.2011.00427.x>, 2012.
- La Mesa, M., Eastman, J. T., and Vacchi, M.: The role of notothenioid fish in the food web of the Ross Sea shelf

- 760 waters: a review, *Polar Biol*, 27, 321–338, <https://doi.org/10.1007/s00300-004-0599-z>, 2004.
- 765 [McMahon, C. R., Roquet, F., Baudel, S., Belbeoch, M., Bestley, S., Blight, C., Boehme, L., Carse, F., Costa, D. P., Fedak, M. A., Guinet, C., Harcourt, R., Heslop, E., Hindell, M. A., Hoenner, X., Holland, K., Holland, M., Jaine, F. R. A., Jeanniard du Dot, T., Jonsen, I., Keates, T. R., Kovacs, K. M., Labrousse, S., Lovell, P., Lydersen, C., March, D., Mazloff, M., McKinzie, M. K., Muelbert, M. M. C., O'Brien, K., Phillips, L., Portela, E., Pye, J., Rintoul, S., Sato, K., Sequeira, A. M. M., Simmons, S. E., Tsonotos, V. M., Turpin, V., van Wijk, E., Vo, D., Wege, M., Whoriskey, F. G., Wilson, K., and Woodward, B.: Animal Borne Ocean Sensors – AniBOS – An Essential Component of the Global Ocean Observing System, *Front Mar Sci*, 8, <https://doi.org/10.3389/fmars.2021.751840>, 2021.](#)
- 770 [Meyer, B., Freier, U., Grimm, V., Groeneveld, J., Hunt, B. P. V., Kerwath, S., King, R., Klaas, C., Pakhomov, E., Meiners, K. M., Melbourne-Thomas, J., Murphy, E. J., Thorpe, S. E., Stammerjohn, S., Wolf-Gladrow, D., Auerswald, L., Götz, A., Halbach, L., Jarman, S., Kawaguchi, S., Krumpen, T., Nehrke, G., Ricker, R., Sumner, M., Teschke, M., Trebilco, R., and Yilmaz, N. I.: The winter pack-ice zone provides a sheltered but food-poor habitat for larval Antarctic krill, *Nat Ecol Evol*, 1, 1853–1861, <https://doi.org/10.1038/s41559-017-0368-3>, 2017.](#)
- Mintenbeck, K.: Trophic interactions within high Antarctic shelf communities - Food web structure and the significance of fish, 2008.
- 775 [Nachtsheim, D. A., Ryan, S., Schröder, M., Jensen, L., Oosthuizen, W. C., Bester, M. N., Hagen, W., and Bornemann, H.: Foraging behaviour of Weddell seals \(*Leptonychotes weddellii*\) in connection to oceanographic conditions in the southern Weddell Sea, *Prog Oceanogr*, 173, 165–179, <https://doi.org/10.1016/j.pocean.2019.02.013>, 2019.](#)
- 780 [Oliver, M. A. and Webster, R.: Kriging: a method of interpolation for geographical information systems, *International journal of geographical information systems*, 4, 313–332, <https://doi.org/10.1080/02693799008941549>, 1990.](#) ~~Oliver, M. A. and Webster, R.: International Journal of Geographical Information System Kriging: a method of interpolation for geographical information systems Kriging: a method of interpolation for geographical information systems, INT. J. GEOGRAPHICAL INFORMATION SYSTEMS, 4, 313–332, <https://doi.org/10.1080/02693799008941549>, 1990.~~
- 785 [Orsi, A. H. and Wiederwohl, C. L.: A recount of Ross Sea waters, *Deep Sea Research Part II: Topical Studies in Oceanography*, 56, 778–795, <https://doi.org/10.1016/j.dsr2.2008.10.033>, 2009.](#)
- [Orsi, A. H., Johnson, G. C., and Bullister, J. L.: Circulation, mixing, and production of Antarctic Bottom Water, *Prog Oceanogr*, 43, 55–109, \[https://doi.org/10.1016/S0079-6611\\(99\\)00004-X\]\(https://doi.org/10.1016/S0079-6611\(99\)00004-X\), 1999.](#)
- 790 [Park, S., Thiebot, J.-B., Kim, J.-H., Kim, K. W., Chung, H., and Lee, W. Y.: Mare incognita: Adélie penguins foraging in newly exposed habitat after calving of the Nansen Ice Shelf, *Environ Res*, 201, 111561, <https://doi.org/10.1016/j.envres.2021.111561>, 2021.](#)
- [Pebesma, E. J.: Multivariable geostatistics in S: the gstat package, *Comput Geosci*, 30, 683–691, <https://doi.org/10.1016/J.CAGEO.2004.03.012>, 2004.](#)
- 795 [Photopoulou, T., Heerah, K., Pohle, J., and Boehme, L.: Sex-specific variation in the use of vertical habitat by a resident Antarctic top predator, *Proceedings of the Royal Society B: Biological Sciences*, 287, 20201447, <https://doi.org/10.1098/rspb.2020.1447>, 2020.](#)
- [Pinheiro, J., Bates, D., and R Core Team: nlme: Linear and Nonlinear Mixed Effects Models, <https://CRAN.R-project.org/package=nlme>, 2022.](#)
- 800 [Piñones, A., Hofmann, E. E., Costa, D. P., Goetz, K., Burns, J. M., Roquet, F., Dinniman, M. S., and Klinck, J. M.: Hydrographic variability along the inner and mid-shelf region of the western Ross Sea obtained using instrumented seals, *Prog Oceanogr*, 174, 131–142, <https://doi.org/10.1016/j.pocean.2019.01.003>, 2019.](#)
- [Plötz, J., Ekau, W., and Reijnders, P. J. H.: Diet of Weddell Seals *Leptonychotes Weddellii* at Vestkapp, Eastern](#)

- 805 [Weddell Sea \(antarctica\), in Relation to Local Food Supply, Marine Mammal Science, 7, 136–144, https://doi.org/10.1111/j.1748-7692.1991.tb00560.x, 1991.](https://doi.org/10.1111/j.1748-7692.1991.tb00560.x)
[Plotz, J., Ekau, W., and Reijnders, P. J. H.: DIET OF WEDDELL SEALS LEPTONYCHOTES WEDDELLII AT VESTKAPP, EASTERN WEDDELL SEA \(ANTARCTICA\), IN RELATION TO LOCAL FOOD SUPPLY, Mar Mamm Sci, 7, 136–144, https://doi.org/10.1111/j.1748-7692.1991.tb00560.x, 1991.](https://doi.org/10.1111/j.1748-7692.1991.tb00560.x)
- 810 [Rignot, E., Jacobs, S., Mouginot, J., and Scheuchl, B.: Ice-shelf melting around antarctica, Science, 341, 266–270, https://doi.org/10.1126/science.1235798, 2013.](https://doi.org/10.1126/science.1235798)
[Rignot, E., Jacobs, S., Mouginot, J., and Scheuchl, B.: Ice-shelf melting around antarctica, Science \(1979\), 341, 266–270, https://doi.org/10.1126/SCIENCE.1235798/SUPPL_FILE/RIGNOT.SM.PDF, 2013.](https://doi.org/10.1126/SCIENCE.1235798/SUPPL_FILE/RIGNOT.SM.PDF)
- 815 Rignot, E., Mouginot, J., Scheuchl, B., van den Broeke, M., van Wessem, M. J., and Morlighem, M.: Four decades of Antarctic Ice Sheet mass balance from 1979–2017, Proceedings of the National Academy of Sciences, 116, 1095–1103, <https://doi.org/10.1073/pnas.1812883116>, 2019.
- Robison, B. H.: What drives the diel vertical migrations of Antarctic midwater fish?, Journal of the Marine Biological Association of the United Kingdom, 83, 639–642, <https://doi.org/10.1017/S0025315403007586h>, 2003.
- 820 Roquet, F., Charrassin, J.-B., Marchand, S., Boehme, L., Fedak, M., Reverdin, G., and Guinet, C.: Delayed-Mode Calibration of Hydrographic Data Obtained from Animal-Borne Satellite Relay Data Loggers, J Atmos Ocean Technol, 28, 787–801, <https://doi.org/10.1175/2010JTECHO801.1>, 2011.
- Rusciano, E., Budillon, G., Fusco, G., and Spezie, G.: Evidence of atmosphere–sea ice–ocean coupling in the Terra Nova Bay polynya (Ross Sea—Antarctica), Cont Shelf Res, 61–62, 112–124, <https://doi.org/10.1016/j.csr.2013.04.002>, 2013.
- 825 Sahade, R., Lagger, C., Torre, L., Momo, F., Monien, P., Schloss, I., Barnes, D. K. A., Servetto, N., Tarantelli, S., Tatián, M., Zamboni, N., and Abele, D.: Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem, Sci Adv, 1, <https://doi.org/10.1126/sciadv.1500050>, 2015.
- Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., and Fraser, W. R.: How Do Polar Marine Ecosystems Respond to Rapid Climate Change?, Science (1979), 328, 1520–1523, <https://doi.org/10.1126/science.1185779>, 2010.
- 830 Sedwick, P. N. and Ditullio, G. R.: Regulation of algal blooms in Antarctic Shelf Waters by the release of iron from melting sea ice, Geophys Res Lett, 24, 2515–2518, <https://doi.org/10.1029/97GL02596>, 1997.
- 835 [Siegelman, L., Roquet, F., Mensah, V., Rivière, P., Pauthenet, E., Picard, B., and Guinet, C.: Correction and Accuracy of High- and Low-Resolution CTD Data from Animal-Borne Instruments, Journal of Atmospheric and Oceanic Technology, 36, 745–760, https://doi.org/10.1175/JTECH-D-18-0170.1, 2019.](https://doi.org/10.1175/JTECH-D-18-0170.1)
- Silvano, A., Foppert, A., Rintoul, S. R., Holland, P. R., Tamura, T., Kimura, N., Castagno, P., Falco, P., Budillon, G., Haumann, F. A., Naveira Garabato, A. C., and Macdonald, A. M.: Recent recovery of Antarctic Bottom Water formation in the Ross Sea driven by climate anomalies, Nat Geosci, 13, 780–786, <https://doi.org/10.1038/s41561-020-00655-3>, 2020.
- 840 [Silvano, A., Purkey, S., Gordon, A. L., Castagno, P., Stewart, A. L., Rintoul, S. R., Foppert, A., Gunn, K. L., Herraiz-Borreguero, L., Aoki, S., Nakayama, Y., Naveira Garabato, A. C., Spingys, C., Akhoudas, C. H., Sallée, J.-B., De Lavergne, C., Abrahamsen, E. P., Meijers, A. J. S., Meredith, M. P., Zhou, S., Tamura, T., Yamazaki, K., Ohshima, K. I., Falco, P., Budillon, G., Hattermann, T., Janout, M. A., Llanillo, P., Bowen, M. M., Darelius, E., Østerhus, S., Nicholls, K. W., Stevens, C., Fernandez, D., Cimoli, L., Jacobs, S. S., Morrison, A. K., Hogg, A. McC., Haumann, F. A., Mashayek, A., Wang, Z., Kerr, R., Williams, G. D., and Lee, W. S.: Observing Antarctic Bottom Water in the](https://doi.org/10.1175/JTECH-D-18-0170.1)
- 845

[Southern Ocean, Front. Mar. Sci., 10, 1221701, https://doi.org/10.3389/fmars.2023.1221701, 2023.](https://doi.org/10.3389/fmars.2023.1221701)

850 [Silvano A, Purkey S, Gordon AL, Castagno P, Stewart AL, Rintoul SR, Foppert A, Gunn KL, Herraiz-Borreguero L, Aoki S, Nakayama Y, Naveira-Garabato AC, Spingys C, Akhondas CH, Salle'e J-B, de Lavergne C, Abrahamsen EP, Meijers-AJS, Meredith MP, Zhou S, Tamura T, Yamazaki K, Ohshima KI, Falco P, Budillon G, Hattermann T, Janout MA, Llanillo P, Bowen MM, Darelius E, Østerhus S, Nicholls KW, Stevens C, Fernandez D, Cimoli L, Jacobs SS, Morrison AK, Hogg AM, Haumann FA, Mashayek A, Wang Z, Kerr R, Williams GD, and Lee WS \(2023\) Observing Antarctic Bottom Water in the Southern Ocean. Front. Mar. Sci. 10:1221701, https://doi.org/10.3389/fmars.2023.1221701.](https://doi.org/10.3389/fmars.2023.1221701)

855 Sipler, R. E. and Connelly, T. L.: Bioavailability of surface dissolved organic matter to aphotic bacterial communities in the Amundsen Sea Polynya, Antarctica, *Elementa: Science of the Anthropocene*, 3, <https://doi.org/10.12952/journal.elementa.000060>, 2015.

860 [Schmidt, K., Atkinson, A., Steigenberger, S., Fielding, S., Lindsay, M. C. M., Pond, D. W., Tarling, G. A., Klevjer, T. A., Allen, C. S., Nicol, S., and Achterberg, E. P.: Seabed foraging by Antarctic krill: Implications for stock assessment, benthic-pelagic coupling, and the vertical transfer of iron, *Limnology and Oceanography*, 56, 1411–1428, https://doi.org/10.4319/lo.2011.56.4.1411, 2011.](https://doi.org/10.4319/lo.2011.56.4.1411)

Smith, W. O., Sedwick, P., Arrigo, K., Ainley, D., and Orsi, A.: The Ross Sea in a Sea of Change, *Oceanography*, 25, 90–103, <https://doi.org/10.5670/oceanog.2012.80>, 2012.

865 Smith, W. O., Tozzi, S., Long, M. C., Sedwick, P. N., Peloquin, J. A., Dunbar, R. B., Hutchins, D. A., Kolber, Z., and DiTullio, G. R.: Spatial and temporal variations in variable fluorescence in the Ross Sea (Antarctica): Oceanographic correlates and bloom dynamics, *Deep Sea Research Part I: Oceanographic Research Papers*, 79, 141–155, <https://doi.org/10.1016/j.dsr.2013.05.002>, 2013.

Smith, W. O., Ainley, D. G., Arrigo, K. R., and Dinniman, M. S.: The Oceanography and Ecology of the Ross Sea, *Ann Rev Mar Sci*, 6, 469–487, <https://doi.org/10.1146/annurev-marine-010213-135114>, 2014.

[SMRU Instrumentation: https://www.smru.st-andrews.ac.uk/Instrumentation/CTD/](https://www.smru.st-andrews.ac.uk/Instrumentation/CTD/), last access: 20 May 2024

870 Speakman, C. N., Hoskins, A. J., Hindell, M. A., Costa, D. P., Hartog, J. R., Hobday, A. J., and Arnould, J. P. Y.: Environmental influences on foraging effort, success and efficiency in female Australian fur seals, *Scientific Reports* 2020 10:1, 10, 1–16, <https://doi.org/10.1038/s41598-020-73579-y>, 2020.

Sutton, T. T.: Vertical ecology of the pelagic ocean: classical patterns and new perspectives, *J Fish Biol*, 83, 1508–1527, <https://doi.org/10.1111/jfb.12263>, 2013.

875 Thomas, G., Purkey, S. G., Roemmich, D., Foppert, A., and Rintoul, S. R.: Spatial Variability of Antarctic Bottom Water in the Australian Antarctic Basin From 2018–2020 Captured by Deep Argo, *Geophys Res Lett*, 47, <https://doi.org/10.1029/2020GL089467>, 2020.

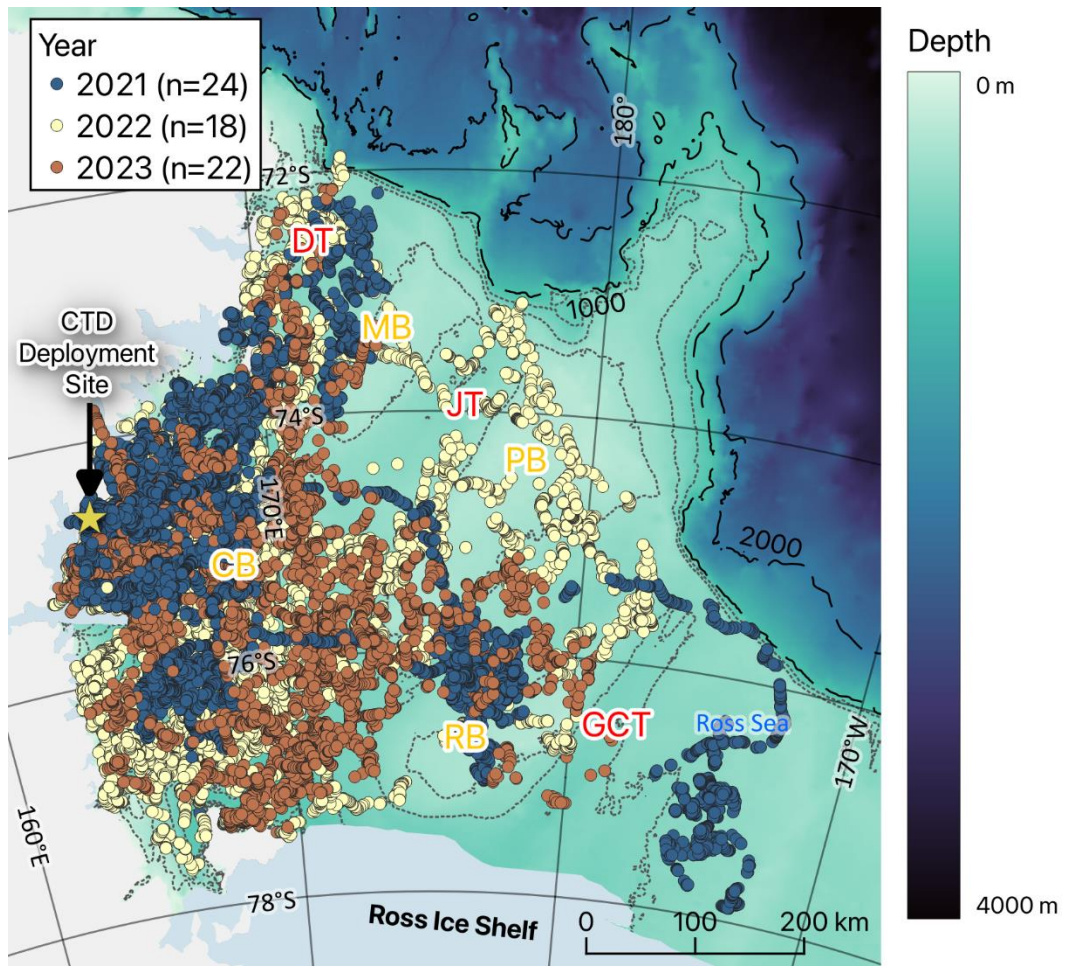
880 Treasure, A., Roquet, F., Ansoorge, I., Bester, M., Boehme, L., Bornemann, H., Charrassin, J.-B., Chevallier, D., Costa, D., Fedak, M., Guinet, C., Hammill, M., Harcourt, R., Hindell, M., Kovacs, K., Lea, M.-A., Lovell, P., Lowther, A., Lydersen, C., McIntyre, T., McMahon, C., Muelbert, M., Nicholls, K., Picard, B., Reverdin, G., Trites, A., Williams, G., and de Bruyn, P. J. N.: Marine Mammals Exploring the Oceans Pole to Pole: A Review of the MEOP Consortium, *Oceanography*, 30, 132–138, <https://doi.org/10.5670/oceanog.2017.234>, 2017.

885 [Viviant, M., Trites, A. W., Rosen, D. A. S., Monestiez, P., and Guinet, C.: Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers, *Polar Biology*, 33, 713–719, https://doi.org/10.1007/s00300-009-0750-y, 2010.](https://doi.org/10.1007/s00300-009-0750-y)

[Viviant, M., Trites, A. W., Rosen, D. A. S., Monestiez, P., and Guinet, C.: Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers, *Polar Biol*, 33, 713–719, https://doi.org/10.1007/S00300-009-0750-Y/TABLES/1, 2010.](https://doi.org/10.1007/S00300-009-0750-Y/TABLES/1)

- 890 Volpov, B. L., Hoskins, A. J., Battaile, B. C., Viviant, M., Wheatley, K. E., Marshall, G., Abernathy, K., and Arnould, J. P. Y.: Identification of Prey Captures in Australian Fur Seals (*Arctocephalus pusillus doriferus*) Using Head-Mounted Accelerometers: Field Validation with Animal-Borne Video Cameras, *PLoS One*, 10, e0128789, <https://doi.org/10.1371/JOURNAL.PONE.0128789>, 2015.
- ~~Wartzok, D., Elsner, R., Stone, H., Kelly, B. P., and Davis, R. W.: Under-ice movements and the sensory basis of hole finding by ringed and Weddell seals, *Can. J. Zool.*, 70, 1712–1722, <https://doi.org/10.1139/z92-238>, 1992.~~
- 895 ~~Wartzok, D., Elsner, R., Stone, H., Kelly, B. P., and Davis, R. W.: Under-ice movements and the sensory basis of hole finding by ringed and Weddell seals, <https://doi.org/10.1139/z92-238>, 70, 1712–1722, <https://doi.org/10.1139/z92-238>, 2011.~~
- Watanabe, Y. Y. and Takahashi, A.: Linking animal-borne video to accelerometers reveals prey capture variability, *Proc Natl Acad Sci U S A*, 110, 2199–2204, https://doi.org/10.1073/PNAS.1216244110/SUPPL_FILE/SM06.MOV, 2013.
- 900 ~~Wheatley, K. E., Bradshaw, C. J. A., Davis, L. S., Harcourt, R. G., and Hindell, M. A.: Influence of Maternal Mass and Condition on Energy Transfer in Weddell Seals, *Journal of Animal Ecology*, 75, 724–733, 2006.~~
- Wheatley, K. E., Bradshaw, C. J. A., Harcourt, R. G., and Hindell, M. A.: Feast or famine: evidence for mixed capital–income breeding strategies in Weddell seals, *Oecologia*, 155, 11–20, <https://doi.org/10.1007/s00442-007-0888-7>, 2008.
- 905 ~~Ydesen, K. S., Wisniewska, D. M., Hansen, J. D., Beedholm, K., Johnson, M., and Madsen, P. T.: What a jerk: Prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*), *Journal of Experimental Biology*, 217, 2239–2243, <https://doi.org/10.1242/JEB.100016>, ~~VIDEO-1~~, 2014.~~
- Yoon, S. T. and Lee, W. Y.: Quality Control Methods for CTD Data Collected by Using Instrumented Marine Mammals: A Review and Case Study, *Ocean and Polar Research* 2021 43:4, 43, 321–334, <https://doi.org/10.4217/OPR.2021.43.4.321>, 2021.
- 910 Yoon, S. T., Sang Lee, W., Stevens, C., Jendersie, S., Nam, S. H., Yun, S., Yeon Hwang, C., Il Jang, G., and Lee, J.: Variability in high-salinity shelf water production in the Terra Nova Bay polynya, Antarctica, *Ocean Science*, 16, 373–388, <https://doi.org/10.5194/os-16-373-2020>, 2020.
- 915 Zheng, Y., Heywood, K. J., Webber, B. G. M., Stevens, D. P., Biddle, L. C., Boehme, L., and Loose, B.: Winter seal-based observations reveal glacial meltwater surfacing in the southeastern Amundsen Sea, *Communications Earth & Environment*, 2, <https://doi.org/10.1038/s43247-021-00111-z>, 2021.

920



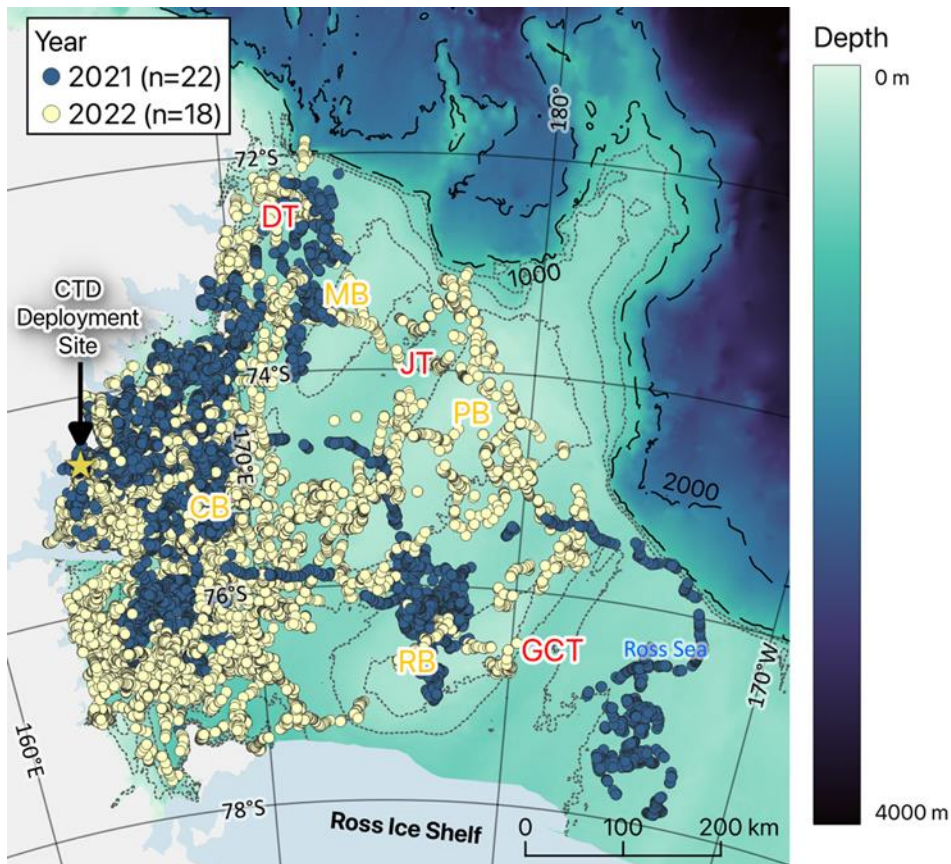
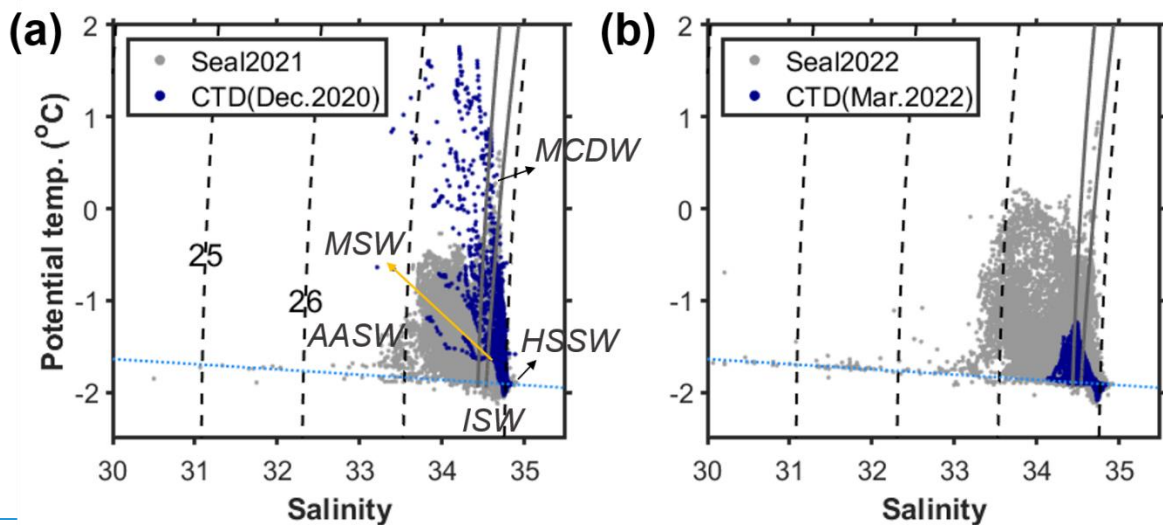
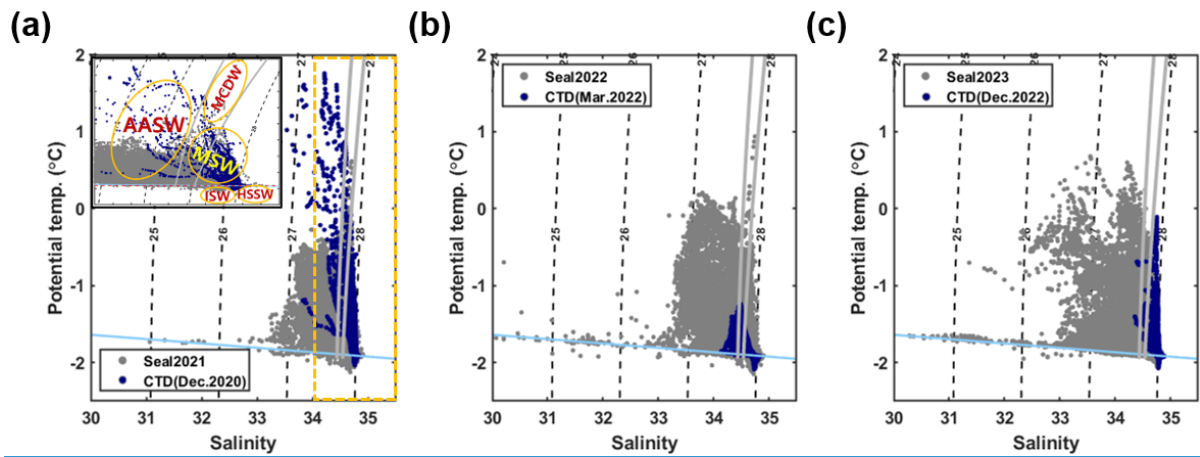


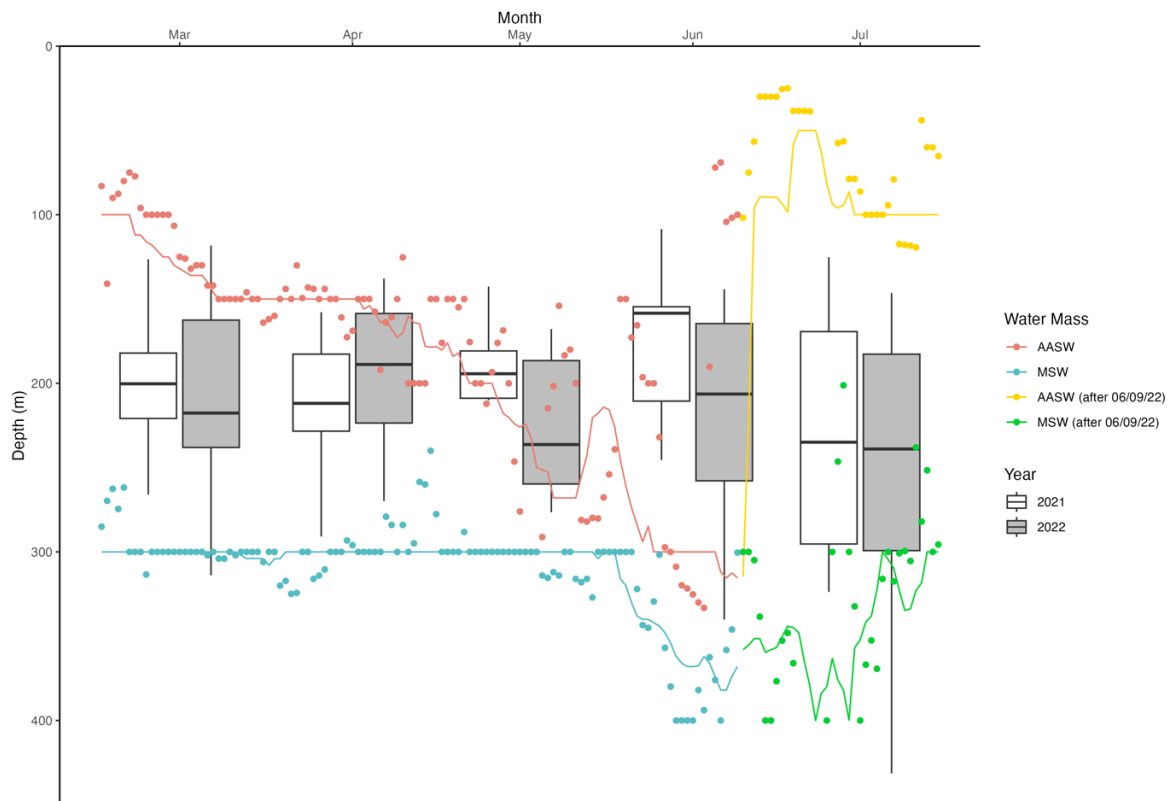
Figure 111. Dive locations of seals tagged at Terra Nova Bay in the Ross Sea (blue, yellow, and brown dots indicated seal ARGOS locations in 2021 and yellow dots indicate the locations in 2022, and 2023, respectively). The abbreviations CB, MB, PB, RB, DB, DT, JT, and GCT mean Cray Bank, Mawson Bank, Pannell Bank, Ross Bank, Drygalski Trough, Joides Trough, Glomar Challenger Trough, respectively. The dashed line represents the shelf break (at depths of 1000 and 2000 m), while the dotted line represents bathymetry at 200 m intervals (200-800 m).

925





930 **Figure 2. θ - S diagram from seal tagging data and ship-based data** (a) θ - S diagram for seal tagging data obtained during
 2021 (gray) and ship-based CTD data recorded from 6 to 25 December, 2020 (blue). The dashed black lines indicate isopycnals
 (kg m^{-3}), and solid gray lines represent 28 and 28.27 kg m^{-3} neutral density surfaces. The solid sky-blue dotted blue line
 indicates the surface freezing point depending on the salinity. The inset indicates a zoomed-in plot for the θ - S diagram
 (yellow-green dashed box) and shows the approximate temperature and salinity range of each water mass. The abbreviations
 935 AASW, MCDW, MSW, ISW, and HSSW correspond to Antarctic surface water, modified circumpolar deep water, ice shelf water,
 and high salinity shelf water, respectively; (b) θ - S diagram. Depicts the same information as panel (a), but for seal tagging
 data obtained during 2022 and ship-based CTD data recorded from 15 to 19 March, 2022, and (c) Depicts the same
 information as panel (a), but for seal tagging data obtained during 2023 and ship-based CTD data recorded from 3 to 17
 December, 2022.



940

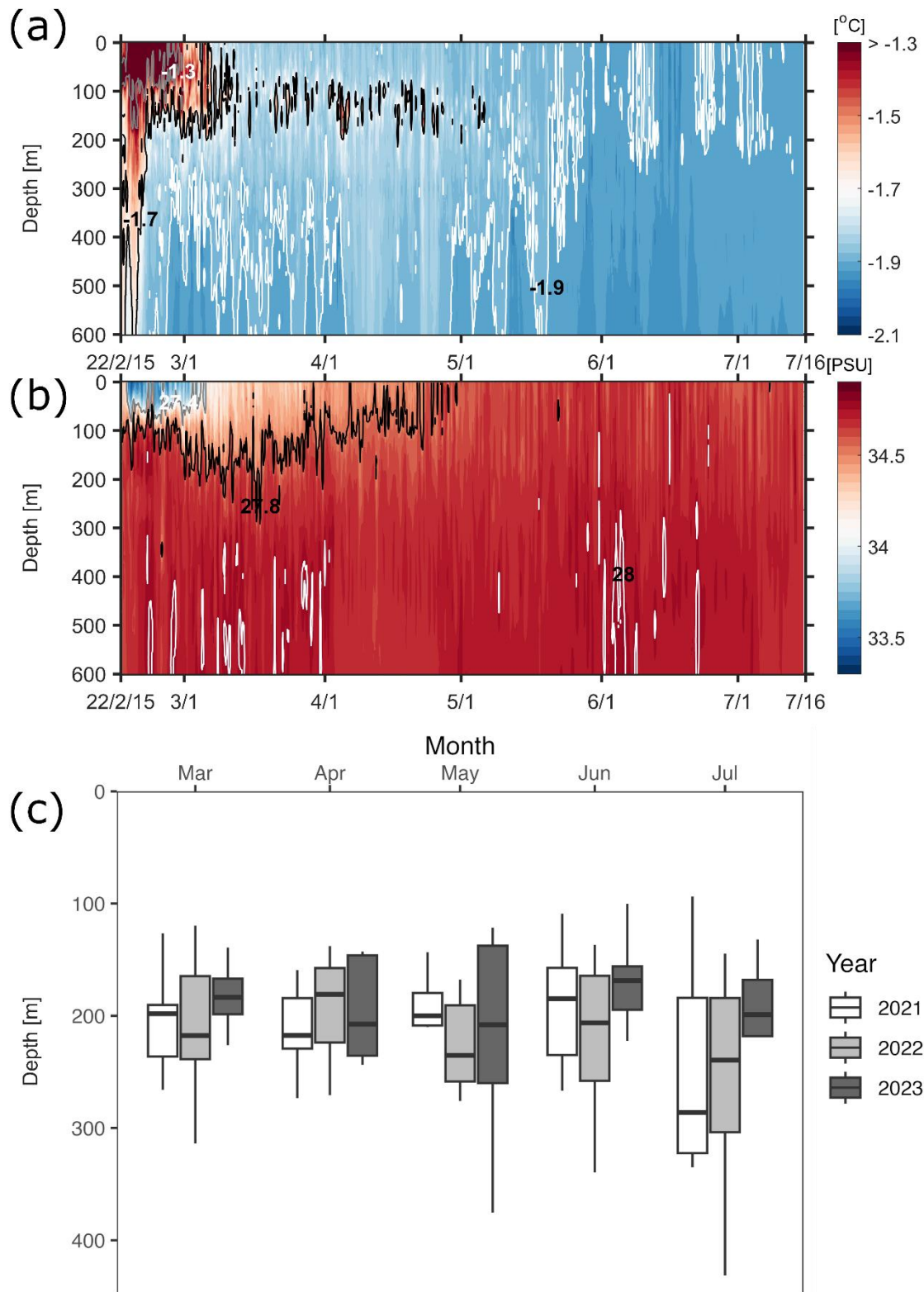
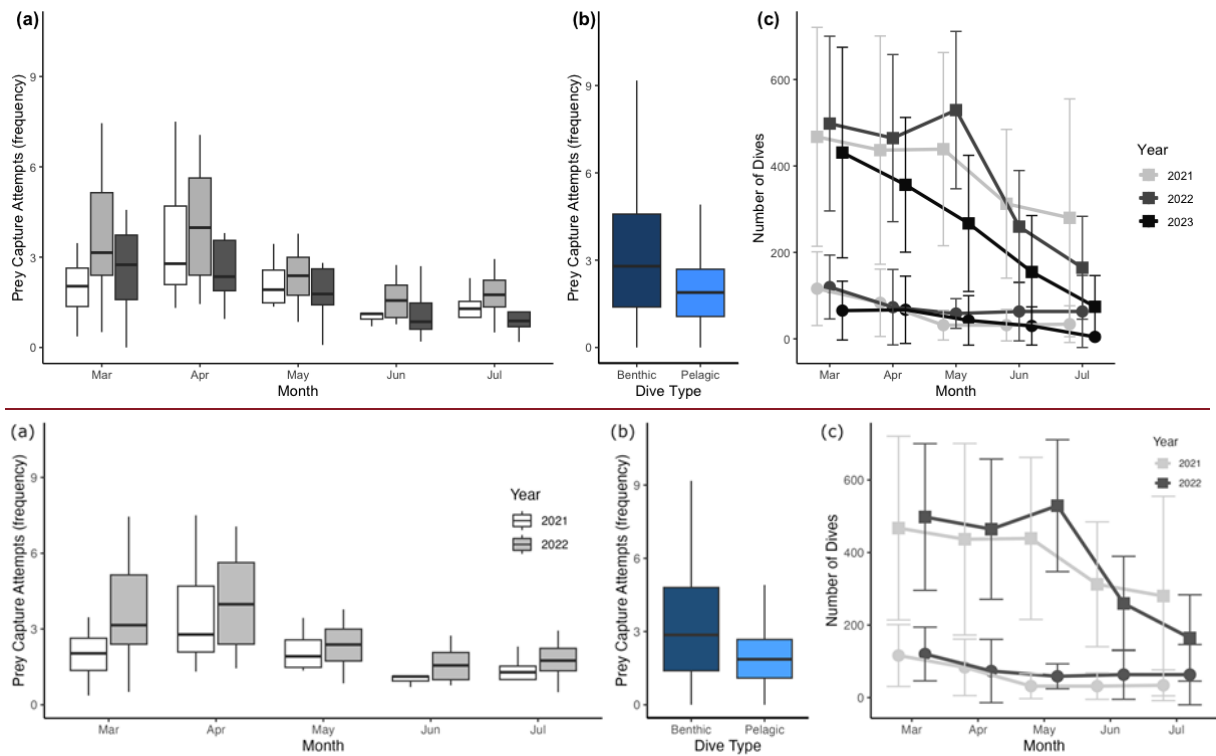


Figure 3. Temporal variation in ~~Weddell seal~~ dive depths of Weddell seals for 2021, 2022 and 2023, with Hovmöller diagram of seawater properties around Terra Nova Bay in 2022 ~~with lower boundaries of Antarctic Surface Water (AASW) and Modified Shelf Water (MSW) based on calibrated data from 2022 only.~~ (a) Hovmöller diagram of potential temperature around Terra Nova Bay. Gray, black, and white solid lines represent -1.3, -1.7, and -1.9 °C isotherms ~~are represented by gray, black, and white solid lines, respectively.~~ (b) Hovmöller diagram of salinity around Terra Nova Bay. Gray, black, and white solid

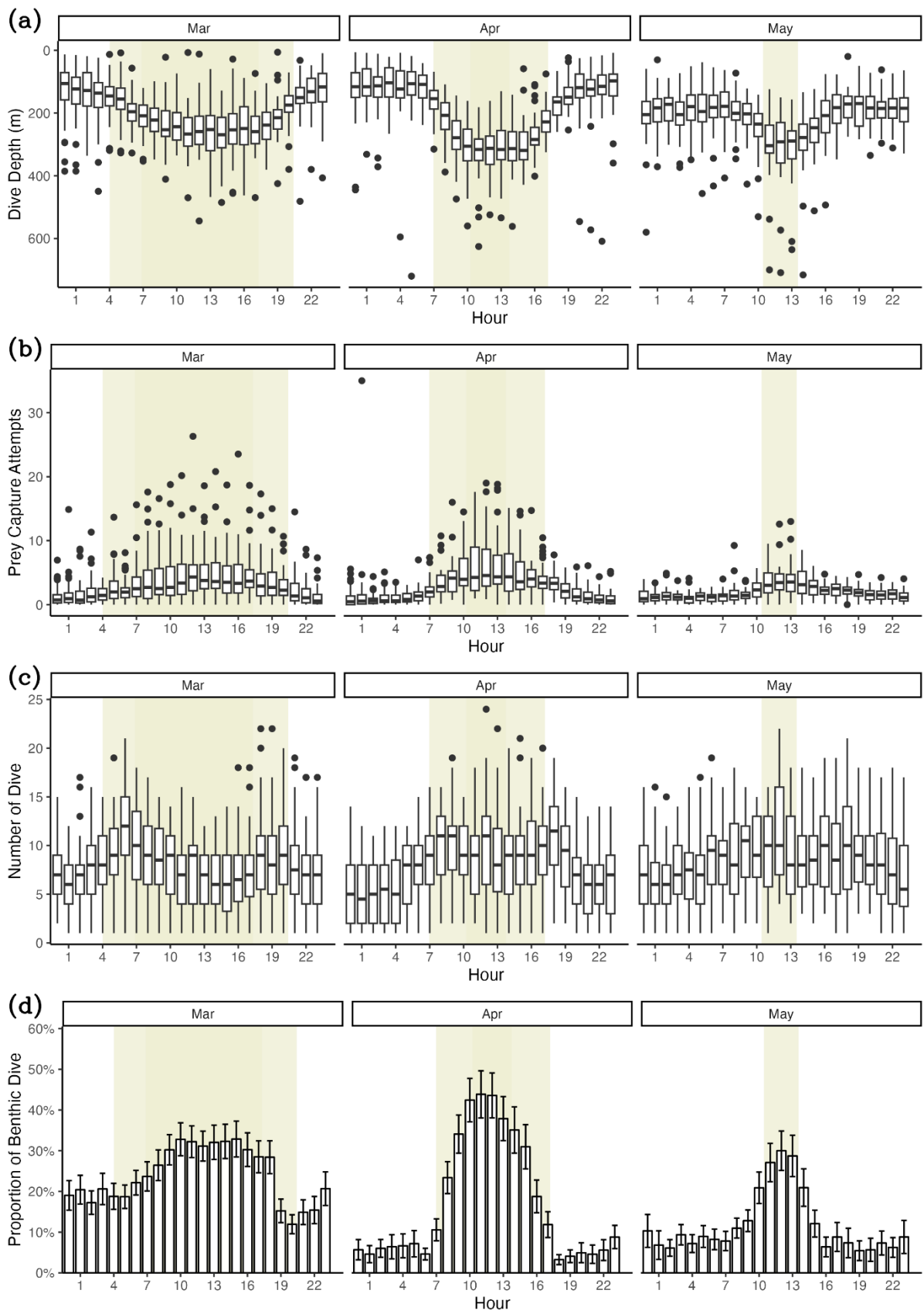
950 lines represent 27.4, 27.8, and 28 kg /m³ isopycnals (σ_θ) are shown by gray, black, and white solid lines, respectively. (ac) White, grey, and black boxes indicate diving behaviors in 2021, 2022, and 2023, respectively, showing a tendency for deeper dives as austral winter approaches. Curves represent the 95th percentile of profiles within a 10-day window, while dots indicate single-day data. Green and blue represent the lower boundaries of MSW and red and yellow represent the lower boundaries of AASW, respectively. Data after June 9 are color coded differently (in green and yellow) due to low reliability from limited observations (3,446 out of 65,013 total). Note that for the water mass data, each month (e.g., 'Mar') corresponds to the first day of that month. (b) Hovmöller diagram of potential temperature around Terra Nova Bay. 1.3, 1.7, and 1.9 °C isotherms are represented by gray, black, and white solid lines, respectively. (c) Hovmöller diagram of salinity around Terra Nova Bay. 27.4, 27.8, and 28 kg/m³ isopycnals (σ_θ) are shown by gray, black, and white solid lines, respectively.

955



960 **Figure 4. Prey capture attempts (PrCA) among (a) seasons (month) and (b) dive types (benthic or pelagic) and seasonal change of the dive frequency.** Prey capture attempts were highest in April and lowest in June. Prey capture attempts were higher in benthic dives compared to pelagic dives. The dark blue box indicates the number of PrCA events per dive during benthic dives, whereas the lighter blue box represents the same statistic during pelagic dives. In (c), curves with square marker represents number of markers represent the total dives and curves with circle marker represents markers represent the number of benthic dives of each month. The error bars represent the mean \pm standard deviation.

965



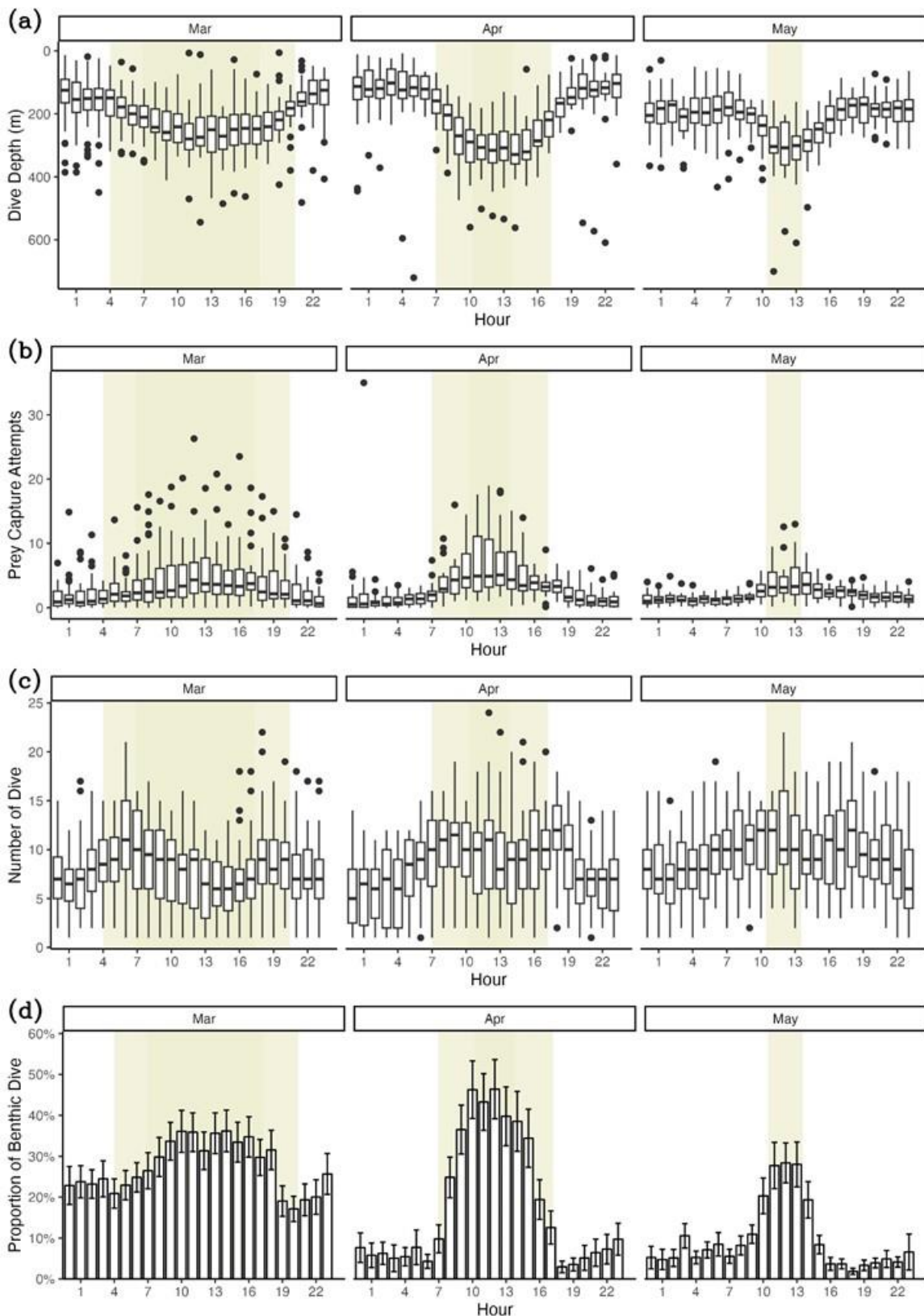
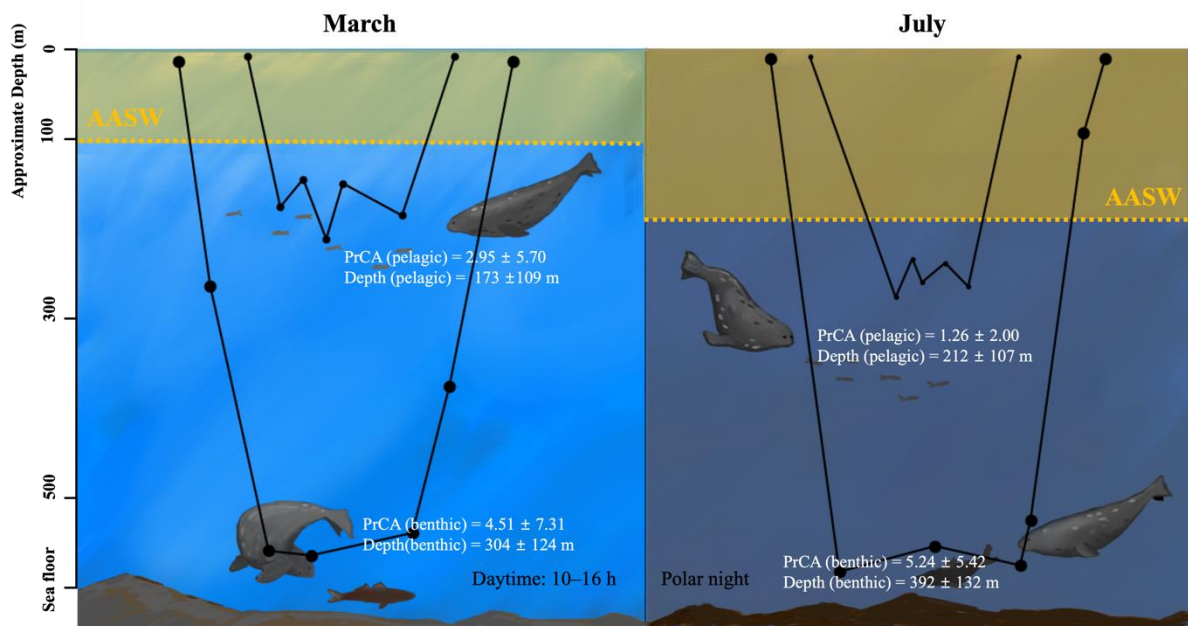


Figure 5. Diel variation in diving behaviors. (a) dive depth, (b) prey capture attempts, (c) number of dives, (d) proportion of benthic dives. The yellow-shaded area denotes the duration of sunlight exposure during the day. The lighter yellow shaded area indicates the period of daylight at the beginning of the month, while the darker yellow shaded area represents the period of daylight at the end of the month.



975 **Figure 6. Schematic summary of seasonal variation in oceanographic conditions and foraging behaviors.** The area shaded
 | in yellow represents the AASW, and the dashed line indicates the lower boundaries. In March, the AASW is positioned at
 | shallower depths, whereas in July, the AASW shifts to deeper locations. AASW is a water mass less preferred by Weddell seals,
 | possibly due to reduced prey availability, which in turn appears to result in deeper dive depths during pelagic dives for
 | Weddell seals. The black line graph in the figure represents typical examples of benthic and pelagic dives in March and July.
 980 The size of the dots is proportional to the PrCA values. PrCA and Depth values are presented as mean ± standard deviation.
 | Note: The high variability of PrCA events results in SD values being larger than the mean values.

Table 1. The Best model for dive depth AIC, BIC, and backward elimination approaches revealed that sex, season (month),
 and year are important variables for predicting prey capture attempts dive depth.

Dive Depth ~ Sex + Season + Year + (1 IID) + corAR1(1 IID)				
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	
<u>(Intercept)</u> <u>(Intercept)</u>	<u>203.79</u> <u>198.21536</u>	<u>181.65 – 225.93</u> <u>185.47 – 210.96</u>	<u><0.001</u> <u><0.001</u>	
<u>Sex [Male]</u> <u>Sex [Male]</u>	<u>-5.97</u> <u>18.09773</u>	<u>-29.08 – 17.13</u> <u>33.32 – 32.88</u>	<u>0.60</u> <u>40.2303</u>	
<u>Season [Apr]</u> <u>Season [Apr]</u>	<u>-9.24</u> <u>-10.04762</u>	<u>-14.96 – -3.53</u> <u>-13.37 – -6.73</u>	<u>0.002</u> <u>0.0025</u>	
<u>Season [May]</u> <u>Season [May]</u>	<u>9.09</u> <u>7.68411</u>	<u>2.91 – 15.27</u> <u>4.17 – 11.2</u>	<u>0.004</u> <u>0.0287</u>	
<u>Season [Jun]</u> <u>Season [Jun]</u>	<u>11.36</u> <u>7.36096</u>	<u>3.57 – 19.15</u> <u>2.95 – 11.77</u>	<u>0.004</u> <u>0.0952</u>	
<u>Season [Jul]</u> <u>Season [Jul]</u>	<u>44.16</u> <u>40.2231</u>	<u>33.91 – 54.41</u> <u>34.81 – 45.64</u>	<u><0.001</u> <u><0.001</u>	
<u>Year [2022]</u> <u>Year [2022]</u>	<u>9.63</u> <u>1.98895</u>	<u>-17.26 – 36.53</u> <u>-12.7 – 16.67</u>	<u>0.47</u> <u>30.8932</u>	
<u>Year [2023]</u>	<u>-9.85</u>	<u>-38.74 – 19.04</u>	<u>0.495</u>	
<u>N IID</u> <u>N IID</u>	<u>44</u> <u>33</u>			
<u>Observations</u> <u>Observations</u>	<u>596</u> <u>7548799</u>			

Table 2. Post hoc (Tukey HSD) test for the "Season" variable included in the best model for dive depth

<u>Group 1</u>	<u>Group 2</u>	<u>Mean Difference</u> <u>(Group 2 - Group 1)</u>	<u>Standard Error</u>	<u>Z value</u>	<u>Pr(> z)</u>
<u>Mar</u>	<u>Apr</u>	<u>-9.245</u>	<u>2.916</u>	<u>-3.17</u>	<u>0.0124</u>
	<u>May</u>	<u>9.089</u>	<u>3.151</u>	<u>2.884</u>	<u>0.03</u>
	<u>Jun</u>	<u>11.358</u>	<u>3.974</u>	<u>2.858</u>	<u>0.0323</u>
	<u>Jul</u>	<u>44.16</u>	<u>5.23</u>	<u>8.443</u>	<u><0.001</u>
<u>Apr</u>	<u>May</u>	<u>18.334</u>	<u>3.175</u>	<u>5.775</u>	<u><0.001</u>
	<u>Jun</u>	<u>20.603</u>	<u>4.006</u>	<u>5.143</u>	<u><0.001</u>
	<u>Jul</u>	<u>53.405</u>	<u>5.262</u>	<u>10.149</u>	<u><0.001</u>
<u>May</u>	<u>Jun</u>	<u>2.268</u>	<u>4.024</u>	<u>0.564</u>	<u>0.9791</u>
	<u>Jul</u>	<u>35.07</u>	<u>5.28</u>	<u>6.642</u>	<u><0.001</u>
<u>Jun</u>	<u>Jul</u>	<u>32.802</u>	<u>5.661</u>	<u>5.794</u>	<u><0.001</u>

Table 23. The best model for prey capture attempts AIC, BIC, and backward elimination approaches revealed that water mass type, season (month), and dive type (benthic or pelagic) are important variables for predicting prey capture attempts.

$$\log(\text{PCA_BTM} + 1) \sim \text{Water Mass} + \text{Dive Type} + \text{Season} + (1 | \text{IID}) + \text{corAR1}(1 | \text{IID})$$

<u>Predictors</u>	<u>Estimates</u>	<u>CI</u>	<u>p</u>
<u>(Intercept)</u> (Intercept)	<u>0.590</u> 0.8	<u>0.51 - 0.66</u> 0.54 - 1.05	<u><0.001</u> <0.001
<u>Water Mass [HSSW]</u> Water Mass [ISW]	<u>0.480</u> 0.04	<u>0.32 - 0.65</u> 0.20 - 0.29	<u><0.001</u> 0.735
<u>Water Mass [ISW]</u> Water Mass [MSW]	<u>0.310</u> 0.07	<u>0.27 - 0.35</u> 0.18 - 0.31	<u><0.001</u> 0.6
<u>Water Mass [MSW]</u> Water Mass [AASW]	<u>0.31</u> 0.18	<u>0.28 - 0.33</u> 0.42 - 0.07	<u><0.001</u> 0.156
<u>Dive Type [Benthic]</u> Dive Type [Benthic]	<u>0.240</u> 0.26	<u>0.22 - 0.26</u> 0.24 - 0.28	<u><0.001</u> <0.001
<u>Season [Apr]</u> Season [Apr]	<u>0.040</u> 0.1	<u>0.00 - 0.07</u> 0.06 - 0.14	<u>0.044</u> <0.001
<u>Season [May]</u> Season [May]	<u>-0.11</u> 0.05	<u>-0.15 - -0.07</u> 0.10 - 0.01	<u><0.001</u> 0.014
<u>Season [Jun]</u> Season [Jun]	<u>-0.31</u> 0.25	<u>-0.36 - -0.26</u> 0.31 - 0.20	<u><0.001</u> <0.001
<u>Season [Jul]</u> Season [Jul]	<u>-0.18</u> 0.1	<u>-0.25 - -0.12</u> 0.17 - 0.03	<u><0.001</u> 0.004
<u>N IID</u> N IID	<u>46</u> 33		
<u>Observations</u> Observations	<u>62317</u> 48799		

Table 3. Post hoc (Tukey HSD) test for “Season” variable included in the best model for dive depth

Group 1	Group 2	Mean Difference (Group 2 – Group 1)	Standard Error	Z value	Pr(> z)
<u>Mar</u> <u>Mar</u>	<u>Apr</u> <u>Apr</u>	<u>-9.245</u> <u>-10.0476</u>	<u>2.9163</u> <u>.3225</u>	<u>-3.17</u> <u>-3.024</u>	<u>0.01240</u> <u>0.0199</u>
	<u>May</u> <u>May</u>	<u>9.0897</u> <u>.6841</u>	<u>3.1513</u> <u>.5134</u>	<u>2.8842</u> <u>.187</u>	<u>0.030</u> <u>.1773</u>
	<u>Jun</u> <u>Jun</u>	<u>11.3587</u> <u>.361</u>	<u>3.9744</u> <u>.4112</u>	<u>2.8581</u> <u>.669</u>	<u>0.03230</u> <u>.443</u>
	<u>Jul</u> <u>Jul</u>	<u>44.1640</u> <u>.2231</u>	<u>5.235</u> <u>.4133</u>	<u>8.4437</u> <u>.43</u>	<u><0.001</u> <u><0.001</u>
<u>Apr</u> <u>Apr</u>	<u>May</u> <u>May</u>	<u>18.33417</u> <u>.7317</u>	<u>3.1753</u> <u>.5504</u>	<u>5.7754</u> <u>.994</u>	<u><0.001</u> <u><0.001</u>
	<u>Jun</u> <u>Jun</u>	<u>20.60317</u> <u>.4086</u>	<u>4.0064</u> <u>.4684</u>	<u>5.1433</u> <u>.896</u>	<u><0.001</u> <u><0.001</u>
	<u>Jul</u> <u>Jul</u>	<u>53.40550</u> <u>.2707</u>	<u>5.2625</u> <u>.4782</u>	<u>10.1499</u> <u>.177</u>	<u><0.001</u> <u><0.001</u>
<u>May</u> <u>May</u>	<u>Jun</u> <u>Jun</u>	<u>2.268</u> <u>-0.3232</u>	<u>4.0244</u> <u>.4502</u>	<u>0.564</u> <u>-0.073</u>	<u>0.97911</u>
	<u>Jul</u> <u>Jul</u>	<u>35.0732</u> <u>.539</u>	<u>5.285</u> <u>.4637</u>	<u>6.6425</u> <u>.956</u>	<u><0.001</u> <u><0.001</u>
<u>Jun</u> <u>Jun</u>	<u>Jul</u> <u>Jul</u>	<u>32.80232</u> <u>.8621</u>	<u>5.6615</u> <u>.919</u>	<u>5.7945</u> <u>.552</u>	<u><0.001</u> <u><0.001</u>

Table 224. Post hoc (Tukey HSD) test for the “Season” variable included in the best model for prey capture attempts

Group 1	Group 2	Mean Difference (Group 2 - Group 1)	Standard Error	Z value	Pr(> z)
<u>Mar</u> <u>Mar</u>	<u>Apr</u> <u>Apr</u>	<u>0.03526</u> <u>-10.0476</u>	<u>0.017523</u> <u>.3225</u>	<u>2.012</u> <u>-3.024</u>	<u>0.24817</u> <u>0.0199</u>
	<u>May</u> <u>May</u>	<u>-0.106787</u> <u>.6841</u>	<u>0.019513</u> <u>.5134</u>	<u>-5.4732</u> <u>.187</u>	<u>< 0.001</u> <u>0.1773</u>
	<u>Jun</u> <u>Jun</u>	<u>-0.308087</u> <u>.361</u>	<u>0.025114</u> <u>.4112</u>	<u>-12.271</u> <u>.669</u>	<u>< 0.001</u> <u>0.443</u>
	<u>Jul</u> <u>Jul</u>	<u>-0.18240</u> <u>.2231</u>	<u>0.033075</u> <u>.4133</u>	<u>-5.5037</u> <u>.43</u>	<u>< 0.001</u> <u><0.001</u>
<u>Apr</u> <u>Apr</u>	<u>May</u> <u>May</u>	<u>-0.1420417</u> <u>.7317</u>	<u>0.019463</u> <u>.5504</u>	<u>-7.2984</u> <u>.994</u>	<u>< 0.001</u> <u><0.001</u>
	<u>Jun</u> <u>Jun</u>	<u>-0.3433417</u> <u>.4086</u>	<u>0.025174</u> <u>.4684</u>	<u>-13.6393</u> <u>.896</u>	<u>< 0.001</u> <u><0.001</u>
	<u>Jul</u> <u>Jul</u>	<u>-0.2172550</u> <u>.2707</u>	<u>0.033185</u> <u>.4782</u>	<u>-6.5489</u> <u>.177</u>	<u>< 0.001</u> <u><0.001</u>
<u>May</u> <u>May</u>	<u>Jun</u> <u>Jun</u>	<u>-0.20131</u> <u>-0.3232</u>	<u>0.025394</u> <u>.4502</u>	<u>-7.929</u> <u>-0.073</u>	<u>< 0.001</u> <u>1</u>
	<u>Jul</u> <u>Jul</u>	<u>-0.0752232</u> <u>.539</u>	<u>0.033335</u> <u>.4637</u>	<u>-2.2575</u> <u>.956</u>	<u>0.15052</u> <u><0.001</u>
<u>Jun</u> <u>Jun</u>	<u>Jul</u> <u>Jul</u>	<u>0.1260932</u> <u>.8621</u>	<u>0.035295</u> <u>.919</u>	<u>3.5735</u> <u>.552</u>	<u>0.00295</u> <u><0.001</u>

995

Table 335. Post hoc (Tukey HSD) test for the “Water Mass” variable included in the best model for prey capture attempts

Group 1	Group 2	Mean Difference (Group 2 - Group 1)	Standard Error	Z value	Pr(> z)
---------	---------	----------------------------------------	----------------	---------	----------

AASW HSSW	HSSW ISW	0.484690 0.04	0.083488 0.12	5.8060 0.34	<0.001 0.98					
	ISW	MSW	0.308249	0.07	0.019305	0.12	15.9670	0.53	<0.001	0.94
	MSW	AASW	0.305366	0.18	0.012401	0.12	24.625	1.42	<0.001	0.44
HSSW	ISW	MSW	-0.176442	0.02	0.083729	0.02	-2.1071	1.47	0.124	0.4
	MSW	AASW	-0.179325	0.22	0.082677	0.02	-2.169	10.72	0.107	<0.001
ISW	MSW	AASW	-0.002883	0.24	0.015478	0.01	-0.186	17.25	0.997	<0.001

Table 446. Regression analyses of dive parameters (dive depths, prey capture attempts per dive, number of dives per day) with respect to the concerning presence of sunlight (day or night).

Dive Depth ~ Day/Night

Predictors	Estimates	CI	P	
(Intercept)	170.17172	157.44 – 182.91	155.94 – 189.00	<0.001
Day boolTRUE	76.479	73.25 – 79.55	76.16 – 83.40	<0.001
N IIDN	4833			
Observations	417333			

log(Prey Capture Attempts + 1) ~ Day/Night

Predictors	Estimates	CI	P	
(Intercept)	0.750	0.67 – 0.83	0.65 – 0.85	<0.001
Day boolTRUE	0.320	0.30 – 0.35	0.31 – 0.37	<0.001
N IIDN	4833			
Observations	417333			

Number of Dives ~ Day/Night

Predictors	Estimates	CI	P	
(Intercept)	17.7519	16.02 – 19.49	18.06 – 19.94	<0.001
is_daytimeTRUE	-1.01	-2.34 – 0.32	-2.17 – 0.7	0.135
N IIDN	4833			
Observations	46143			

Proportion of Benthic Dives ~ Day/Night

Predictors	Estimates	CI	P
(Intercept)	-2.55	-2.87 – -2.24	<0.001

<u>is_daytimeTRUE</u>	<u>1.14</u>	<u>1.06 – 1.21</u>	<u><0.001</u>
<u>N IID</u>	<u>48</u>	—	
<u>Observations</u>	<u>41733</u>	—	—

1000

—